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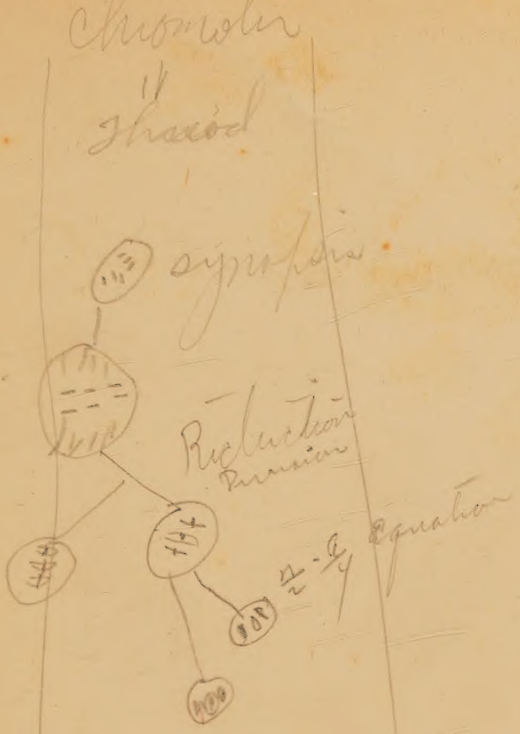

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PRINCIPLES OF ANIMAL BIOLOGY

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FRONTISPIECE.—Three-toed sloth Bradypus, from South America, an example of an animal adapted to arboreal life. The sloth lives in trees, usually suspended from a limb. It cannot support itself on its legs and hence cannot walk on the ground. (*Photograph by A. G. Ruthven.*)

PRINCIPLES
OF
ANIMAL BIOLOGY

BY

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TO

THE TEACHERS OF ZOÖLOGY

WHO HAVE BEHELD THEIR SUBJECT
OUTGROW A PEDAGOGICAL METHOD

215643

PREFACE TO THE THIRD EDITION

The changes that have crept into the order of presentation of the subject matter of the elementary course in zoölogy at this institution make a formal rearrangement of this book desirable. The principal changes of this kind are in that section of the book dealing with morphology and physiology of higher types. Advantage has been taken of this opportunity to make considerable revisions elsewhere. The chapter on genetics has been strengthened, the account of cell division is simplified and made to reflect more accurately the trend of present investigation, and the discussion of cell physiology is, we hope, brought up to date so far as is possible without becoming controversial. Smaller alterations have been introduced at many places. Errors that have come to our attention have been corrected, though doubtless some have been overlooked. The fundamental plan of the book, however, remains the same. The presentation of basic principles and broad generalizations to elementary students is, we still believe, the best approach to the subject.

A. Franklin Shull.

Ann Arbor, Mich.
August, 1929.

ACKNOWLEDGMENTS

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PRINCIPLES OF
ANIMAL BIOLOGY

CHAPTER I

INTRODUCTION

The science of animals, which has long been called *zoölogy*, has undergone, in common with other sciences, a tremendous change over the centuries. Always defined in the same terms, its content has been modified with increasing knowledge. Originally it was concerned largely with the classification and naming of animals. Today, it includes a large body of doctrine concerning modes of life, life processes, interrelations of animals, development, distribution, and descent, most of which has little direct bearing upon classification. In many cases the principles involved are identical, or very similar, in both plants and animals, and the term *biology* is used to designate them. For this reason, some have preferred to call the science that embraces the body of fundamental doctrine just mentioned, as applied to animals, *Animal Biology*. The latter name appears to convey less of the idea of classification, and more of principles, than does the term zoölogy. The name, however, is immaterial if the content of the subject is understood. While this whole book is an attempt to create such an understanding in the uninitiated, it is important that a general perspective of the field be attained at the outset. To this end the major divisions of the science are indicated in the following sections.

Morphology.—The branch of zoölogy dealing with structure is called *morphology*. It has been until recently the chief interest of a large majority of zoölogists. Gross form of the body as a whole, the structure of its parts or organs or systems of organs, the structure of the tissues that make up the organs or bind them together, the structure of the units or cells which compose the tissues, and the structure of the minute components of the cells, are all included in morphology. The structure of embryos, or developmental stages, of animals is as much morphology as is the structure of adults. Various names, such as *anatomy*, *histology*, *cytology*, and *embryology*, have been given to the departments of morphology. They differ from one another in the size and nature or stage of the objects with which they deal, and in the methods of study, but all are primarily concerned with form and structure.

The term anatomy refers literally to the cutting up or dissection of the bodies of animals or plants. Dissection without mechanical or optical aids reveals only the grosser structure, hence early anatomy dealt with such things as the divisions of the brain, the spinal cord, and the larger nerves and ganglia, the stomach and intestine and the larger glands and ducts in connection with them, the chambers of the heart and the arteries and veins, the individual bones of the skeleton, and so on. Description or study of these things is now commonly called gross anatomy. As skill increased and aids to dissection multiplied, more and more minute structures were studied, so that, today, the anatomist considers nothing too minute to fall within his province. As a result the term anatomy has become almost as inclusive as morphology. In practice, nevertheless, certain phases of morphology are still usually designated by other names.

Thus histology deals with the grouping of cells of a given kind into masses or layers called tissues. The epidermis of the skin is composed of cells of the same general kind grouped together; it is therefore a tissue. Muscle and bone are tissues, as are also tendons, many glands, and the components of the nervous system. Cytology is concerned with the minute components of cells, the parts of the nucleus, the minute structure of the living matter, the nature of cell organs, and the like. Embryology has to do with the young or developmental stages of animals. When it is purely descriptive, dealing only with the structures of these young stages, not with the processes going on in them, it is morphological in its nature.

Morphology is historically the oldest of the divisions of zoölogy, since in early times practically all that was known of animals was their structure.

Physiology.—The functions of organs, tissues, and cells, the processes carried on in them, are the subject matter of *physiology*. Not only the more obvious functions, such as digestion, circulation, and respiration, but the obscure chemical reactions involved in growth and repair, belong in this field. The conduction of nerve impulses, the origin of acts of will, the processes of thought, the behavior of animals under given conditions, all are the subject matter of physiology. Ordinarily one thinks of those processes which maintain the animal, get and prepare its food, secure a supply of energy, control repair and growth, or eliminate waste as being physiology. The processes of development in embryos, however, are also included in this branch of zoölogy. The events which initiate the division of an egg, control the folding of cell layers, direct the migration of cells, and govern differential rates of growth in a developing embryo are physiological processes. Embryology thus has a physiological aspect, as well as a purely morphological one.

Physiology is also a very old branch of zoölogy although the subject remained in a crude state long after morphology, particularly the morphology of the higher mammals including man, had become fairly definite.

Ecology.—This branch of zoölogy has to do with the relations of animals to their environment. The necessity for getting food puts an organism into relation to the things about it. Its method of locomotion is intimately related to the medium in which it lives. The presence of enemies and competitors is an almost universal condition of life. The possibilities of rearing young are important in every animal's environment. The very behavior of an organism, especially in lower forms of life, as is pointed out in a later chapter, is dependent upon the nature of the surroundings, so that a minute change in the environment may completely reverse the organism's behavior.

Very often the study of ecology takes the form of determining the factors which govern an animal's choice of *habitat*, or place of abode. Animals of any species are found only or chiefly in certain types of environment, depending partly upon their structure and partly upon their physiological requirements. Often, also, their occurrence in a given environment is dependent on the presence of certain other animals. The factors which induce, or force, an organism to seek an aerial, aquatic, terrestrial, or subterranean abode are often quite obscure. One animal must have a pond, rather than a stream, and not all ponds are equally good; nor is every part of the same pond a suitable place. The reasons for these requirements are partly to be found in the animal, partly in the surroundings; or, more correctly stated, in the relations existing between the factors within the animal and those external to it. Thus, ecology involves much that is morphology and physiology, but only in so far as structure and function relate the organism to other things about it. It is the work of the ecologist to discover the structure and functions of an animal which are of significance in such relations, and the features of the environment to which they are related. Scientific work of this kind has only in comparatively recent years seriously occupied the minds of any considerable number of zoölogists.

Zoögeography.—The geographical distribution of animals, or *zoögeography*, is in some respects closely related to ecology. It deals with distribution, as does ecology, but in a much wider sense. It is concerned with regions, rather than kinds of environment. The regional distribution of a species is limited by the distribution of environments suitable for it, but no species of animal occupies all the regions of the world where the environment is right. Kangaroos, to cite a striking example, are found only in the Australian region, although many other places on the earth have a temperature, humidity, and other features very similar to those of Australia. Presumably kangaroos could live in most of these similar regions if introduced into them, but they are not there. On the contrary, rabbits were entirely wanting in Australia until taken there by man, since which time they have become, like the English sparrow when introduced into America, almost a scourge. The failure of a species

to occupy a region in which the conditions of life are suitable for it usually means that it has been unable to reach that region, and this inability may have been due to the present topography of the region, to its geological history, or to the place of origin of the species. Thus, while zoögeography involves suitability of environment (ecology), it is also concerned with historical factors.

Paleontology.—In *paleontology* the zoölogist studies the animals of the past. Parts of these ancient animals are preserved as fossils in sedimentary rocks. The relative age of the fossils is determined from the relative depth of the rock strata in which they occur. The vast majority of animals, perhaps all of them, living on the earth in these early times were of different species from those alive today. Though there are numerous similarities, only a very few fossil animals were practically identical with living ones and the similarity of even these few must be stated with some reserve. Moreover, the deeper fossils are quite different from those in the upper layers. Past ages on earth were thus marked by very different groups of living beings. All of the problems which exist for animals today presumably existed for those of the past. Those animals had structure and functions, they were related to the environment, and they were distributed over the earth in various ways.

There is thus a zoölogy of the past just as there is a zoölogy of the present. The paleontologist is limited, however, in his study of ancient animals, to what can be discovered from their remains. He is unable to experiment upon his subjects, nor can he rear them in his laboratory. It thus happens that paleontology is mostly concerned with structure and classification of fossil animals, and with their distribution in space and in time. Other things can be inferred concerning them, such as their mode of life, the reasons for their migrations, or their relation to the environment, and such inferences are of much or little value according to the nature of the evidence which supports them. Paleontology is thus a limited sort of zoölogy.

In addition to the above features, which concern the past animals themselves, the paleontologist deals also with the relation of those animals to the animals of today. Whether the early beings were the ancestors of the ones now on earth, and if so, the probable lines of descent; what became of the extinct species and what brought about their extinction; what determined the succession of animals to the present time, these and similar questions of an evolutionary bearing are in the domain of paleontology.

Taxonomy.—The classification of animals, with the principles on which it rests, is known as *taxonomy*. Classification is based on relationship, nearly related animals being placed together in the same group. This relationship is discovered from similarity of structure, from facts of distribution, or from fossils. A group in which the members

are very closely related is apt to be a small one. Such a group can nearly always be shown to have certain similarities to one or more other groups which indicate that they are related to each other. The small groups are thus combined into a larger group of a higher rank, the component small groups still being distinguished from one another. A zoölogist whose chief interest is the classification of animals is usually called a systematic zoölogist. Ordinarily it is possible for one person to be familiar with the minute details of classification in only one group, or in a few groups, not in the whole animal kingdom. One who knows the birds thoroughly may be unqualified to classify reptiles or fishes. A student of insects usually knows insects of all groups in a general way, but can arrange in detail the members of only one order, for example, the butterflies and moths. Systematic zoölogists, having different interests, are called by different names. The student of birds is an *ornithologist;* of the insects, an *entomologist;* of the reptiles, a *herpetologist.* Systematic zoölogists may appear to have little in common; but if their work is well done, it rests in every case upon the relationship believed to exist among the animals of their special groups. That is, they are taxonomists. Although, as stated, one person can usually master the details of classification in only a small part of the animal kingdom, it is not a difficult task to learn the main divisions of all the principal groups of animals, and to be able to place almost any animal at sight in its proper group.

Genetics.—This division of biology deals with heredity, variation, and related phenomena. The name refers literally to the origin of the characteristics of offspring from the characteristics of their parents. The features of an animal or plant may be transmitted more or less independently of one another, so that characters of both parents may be combined in a variety of ways in the children, and the offspring may differ among themselves. Somewhat definite laws are followed in the assortment of parental characters, and to discover these is the work of the geneticist. Knowledge of genetics and discoveries in this field require an acquaintance with the cells which are responsible for reproduction, and with their complicated behavior; a knowledge of the process of development by which offspring arise; and a familiarity with the influences of environment and of internal agencies in the modification of visible characters. It would be possible, therefore, to divide genetics into several parts which could be distributed to the fields of morphology, physiology, and evolution. Many biologists, however, are interested in the method of transmission of inherited characters, though not primarily interested in either structure or function or evolutionary change as such. They approach the problem of inheritance by experiments in hybridization, supplemented by cytological and embryological studies.

Evolution.—Evolution is the gradual change of species through successive generations. Animals of today are not like those of a few million years ago, as is clearly proven by fossils. Since present-day animals must have decended from ancient forms, somewhere in the intervening generations offspring must have been unlike their parents. The difference may have been small or large, and may have occurred at frequent intervals or rarely. Supporting evidence of such changes is found in nearly every branch of zoölogy. Paleontology furnishes such evidence in the differences between animals of successive geological periods. Many facts of distribution are readily explained only by assuming evolution. The study of morphology and physiology, by revealing similarities between different animals, indicates their relationship through a common origin, and the whole science of taxonomy has its basis in change with descent. Evolution is not, then, an isolated science, but is closely bound up with morphology, physiology, genetics, taxonomy, zoögeography, and paleontology; for in each of these fields valuable evidence of evolution is found, and the explanation of evolution and evidence of the course which it has taken are important parts of them all.

Summary and Comparison.—The eight fields of knowledge described in the foregoing paragraphs may be called the zoölogical sciences. Every fact of zoölogy may be referred to one or another of these subjects. They are not wholly distinct from one another, however, for not infrequently a single fact belongs to two or more of the sciences. That is, the fields overlap. The merging of evolution into the other problems of genetics, paleontology, zoögeography, taxonomy, and others has been pointed out. Ecology may very largely deal with physiological relations. Physiological facts are in most instances also morphological ones, since it is usually difficult to separate functions from the structures in which they are manifested. This overlapping and the merging of one subject into another, far from being confusing, is eloquent testimony of the unity of the whole field of zoölogy. There is also a unity of zoölogy and botany, which is the science of plants, for in botany the same subdivisions exist. There is a morphology, a taxonomy, an ecology, and an evolution of plants; and but for the differences in the modes of life of plants, the principles involved are largely the same as for animals. Paleontology and zoögeography also have their counterparts in botany. This book, being a general discussion, will contain elementary facts and principles from each of the branches of the science.

Although zoölogy of today comprises the eight sciences mentioned above, it would be a mistake to suppose that it has always been so inclusive. Some of the branches are much older than others. Morphology, as has been stated, is very ancient, while ecology is a mere infant. Physiology has been known for centuries, while the contemplation of evolution has been common for but seventy years. Zoölogy, then, has a

history, a knowledge of which is useful in accounting for its present content and tendencies.

Conditions of Early Biology.—One who reads of the early ideas regarding animals is apt to conclude that the science of zoölogy was much better developed among the early philosophers than it really was. The list of early writers who published biological doctrines is a long one, but many of these doctrines were only a very small part of the works in which they were contained, and the authors were often chiefly interested in religion, or theology, or astronomy, with their biological concern largely incidental. Moreover, these writings were often based, not upon observation or experiment, but upon speculation, anecdotes, rumor, or superstition.

Although the ancient knowledge of animals was of little value in comparison with the zoölogy of today, the early students of the science should be regarded with lenience. Their advantages were meager. They could not be taught the subject, for they were pioneers. A sophomore now may know more about animals than did Aristotle, even though in intellect he would appear, beside Aristotle, as a candle to the sun. The absence of microscopes and other equipment closed many of the doors of investigation that are open now even to elementary students. Hence, while recognizing that ancient zoölogy was a very inferior science, as judged by modern standards, the early zoölogists must not be too harshly criticized. The best of them are to be credited with accomplishments which, in view of their handicaps, were truly remarkable.

The Early Greeks.—The earliest zoölogical writings that are known were produced by the Greeks. These were not the earliest works, since they contain references to the "ancients," but they are the earliest that have been preserved. The early Greeks were inclined to the deductive method. They reached a conclusion quickly, with little evidence to support it, and then applied their generalization to discover what other things ought to be true. Naturally, if the generalization was incorrect, and it was likely to be incorrect, its application led to fallacies.

Surrounded as Greece is by warm waters, teeming with life, the country furnished abundant material for observation of animals. But the Greeks were of a philosophical bent, they preferred theorizing to the prosaic collection of facts. The origin of things in nature was particularly fascinating. Thales, an astronomer, conceived all life to have orginated in the ocean, an idea that has its supporters today. Anaximander supposed that living things were first produced by the drying crust of the earth, which had been in a liquid state; and curiously enough, man was held to be the first of these products. He also believed that animals, of the kinds we know today, are produced out of inorganic matter, as eels from mud. This doctrine of the origin of living from nonliving matter, known as *abiogenesis*, was held for centuries in the crude

form adopted by the Greeks, but has been long since abandoned. Fossils were recognized as animal remains by Xenophanes, who correctly inferred from them that water once covered the land. Empedocles made some observations on embryonic development, the earliest ones, indeed, that are recorded. He also evolved a theory of the origin of animals, according to which heads, arms, trunks, necks, eyes, etc., were formed separately, and were kept apart at first through the force of hate. Then love triumphed, he supposed, and these parts began to combine. The combinations were purely fortuitous, and most of them were incapable of maintaining themselves. Others were more fortunate, and formed the animals now found on earth. Empedocles thus enunciated a crude form of theory of the survival of the fittest. These writers all lived in, or prior to, the fifth century before Christ.

Aristotle.—One of the Greek philosophers stands out in high relief, by reason of his correct methods and superior accomplishments. This

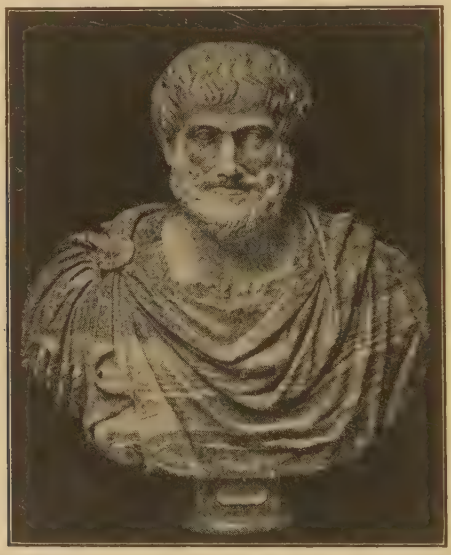

FIG. 1.—Aristotle, 384–322 B. C. (*From Hekler's Greek and Roman Portraits. G. P. Putnam's Sons.*)

was Aristotle (Fig. 1), who lived in the fourth century before Christ. Aristotle was a man of high intellect and one of the greatest philosophers of ancient times. He was a pupil of Plato, and the teacher of Alexander the Great. Like other scholars of his time, he dealt with a great range of subjects and published hundreds of works, many of which are lost. He wrote treatises on philosophy, psychology, metaphysics, rhetoric, and politics, but assumed the rôle of leader most distinctly in natural history. If one were to judge Aristotle by present standards the great philosopher might seem less notable, but it must be remembered that he was a pioneer,

and that he lived at a period in the development of science when errors and crudities were to be expected. However, he recognized the things of importance and he adopted the right method in trying to advance knowledge. He appealed directly to nature for his facts, and founded his natural history chiefly on observation. Far less is it to be said of his successors, as will appear later.

The works of Aristotle contain a number of errors which seem now to be rather obvious. But his insistence on the inductive method, which is today the method of laboratory sciences, far outweighed his occasional failures to use that method properly. He obtained his facts at first hand. Had his errors been twice as numerous as they were, Aristotle would still be the heroic figure of the Greek period of learning, in the field of zoölogy, because he declined to accept authority, except that of nature itself.

Unfortunately, Aristotle represents the greatest development of zoölogy until comparatively recent times. No subsequent naturalist of note arose in Greece. It is to Rome that one must turn for the next famous zoölogist. The only one worthy of mention seems to have been the elder Pliny, soldier and writer, who flourished in the first century of the Christian era, or four hundred years after Aristotle. Pliny, however, did nothing original, he merely compiled the works of others, and was none too judicious in his choice of material.

The Dark Ages.—Learning was entering dark days even in the time of Pliny, and zoölogy shared the fate of her sister sciences. The story of this period is familiar in the annals of every branch of knowledge. Books were scarce, the schools lost their influence, and travel was difficult. Men no longer cared to investigate, they preferred to be told what to think. The clergy fostered this attitude, for they represented authority, and lived upon subservience. Obedience in intellectual as well as religious matters was a customary thing among the laity. Controversies upon insignificant matters, which could easily have been settled by a few first-hand observations, were referred to the books of Aristotle and others for decision. Those who chanced to make observations for themselves, and then found something in their favorite writings which seemed to refute their discoveries, refused to believe their own senses.

The period of deference to authority lasted many centuries. During this time interest in zoölogy was almost confined to the medical schools, where, in the form of anatomy, it had a practical value. But even anatomy was subject to the ills of the time. The works of Galen, a famous Greek anatomist who was born about A.D.130 were the authority on which all teaching of anatomy was based. Galen himself was a talented observer and forceful writer, and it is not occasion for surprise that his works were accepted as the authority in questions of anatomy. He worked under a handicap imposed by the customs of his time,

however, since human bodies could not then legally be dissected. As substitutes, other animals were used, and wherever these animals differed from man Galen was in error. In the absence of better works, Galen's books were read from the lecturer's desk, with occasional demonstrations of dissections—which, be it said, often belied the text they were supposed to illustrate. The negation, however, was never noticed, or perhaps was attributed to improper specimens for demonstration.

The Revival.—Slavish acceptance of authority could scarcely do other than breed revolt, and eventually prove its own undoing. Human

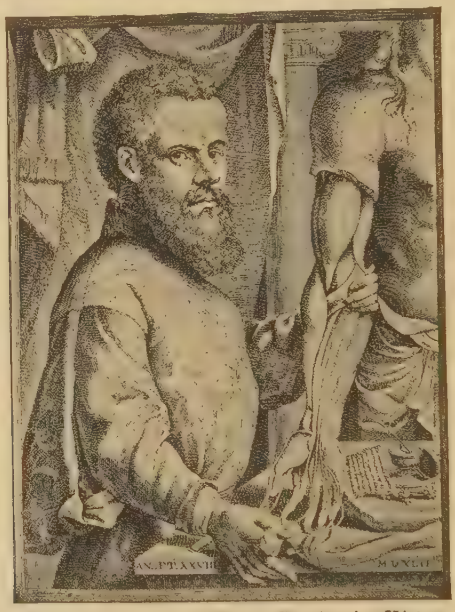

FIG. 2.—Andreas Vesalius, 1514–1564. (*From Garrison's History of Medicine. W. B. Saunders Co.*)

bodies became increasingly accessibile for dissection. And so, after more than a thousand years of servility, one finds Mondino da Luzzi, a professor at the University of Bologna, in Italy, publishing in 1315 a work on human anatomy that was based, not on Galen's books, but on dissection. He dissected as many as three human bodies. Two hundred years later, Berengario, also of the University of Bologna, dissected a hundred or more bodies, and presumably taught anatomy from them.

It was reserved, however, for Vesalius, a gifted Belgian, to make the use of Galen's books alone unfashionable. Vesalius was a native of the city of Brussels, where he was born in 1514. A portrait of him is reproduced in Fig. 2. He appears to have inherited a passion for learning from an ancestry of physicians and scholars. His leaning was toward anatomy, and in his boyhood, besides securing the traditional schooling

in Greek and Latin, he taught himself dissection, using the common animals about him. On entering the University of Paris to study medicine, it is said that he early became dissatisfied with the clumsy manner in which demonstrations were made in the lectures, that he pushed aside the barbers who were making the dissection, and demonstrated the structures himself. After finishing his medical course he was for a time military surgeon, and was then appointed to teach anatomy in the University of Padua in Italy. His teaching began with the time-honored method of reading Galen's books, but the independent spirit which he

FIG. 3.—William Harvey, 1578–1657. (*From Garrison's History of Medicine.*)

displayed in early life compelled him to discontinue the practice. He ended by teaching anatomy only as he himself found it by dissection, and only as he could demonstrate it to his students.

Unlike Mondino da Luzzi and Berengario, Vesalius was able to carry conviction to others. His students and colleagues recognized his worth, and other anatomists were gradually persuaded. Having probably no more facilities of original dissection than did Berengario and other anatomists of his time, Vesalius possessed what they probably lacked, a forceful personality. Opposition of the clergy, who had everything to lose and nothing to gain from a return to observation, did not daunt him. He was as adept in controversy as they—and Vesalius won. He did not live to see his method of appeal to nature universally adopted, but reform was rapid after his time, and to him belongs the chief credit for starting the reform.

The Experimental Method.—At the time of Vesalius zoölogy (anatomy, mostly) was an observational science. Every science has been observational in the early stage of its development. Observation represents on the whole the simplest phase of investigation, since it is possible to observe without any anticipation of the phenomena to be observed. The use of experiment is a later development in each field. It implies

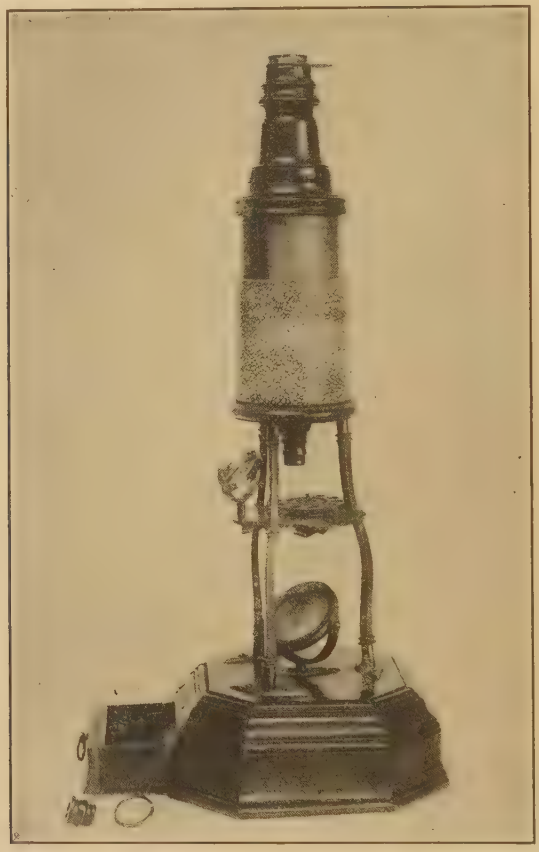

FIG. 4.—An eighteenth century microscope. (*Courtesy of American Museum of Natural History.*)

looking forward to a result, and the experimenter must formulate some problem and adopt a suitable procedure for its solution. Any branch of investigation, therefore, in which the experimental method is applicable may be regarded as mature or youthful, according as experiment has or has not come into common use. At the time of which we write, experiment had long been used in physics and chemistry. Experiment had been used occasionally in zoölogy even as early as Aristotle, but had been long since forgotten as a method. Its restoration was in

large part due to the efforts of William Harvey, of England (1578–1657) (Fig. 3). Harvey is best known as a physiologist, sometimes called the founder of physiology. He is credited with the discovery of the circulation of the blood. One of his chief services to zoölogy, however, was his frequent use of the method of experiment. In his work in physiology he directly affected only one field of zoölogy; but in his adoption of the experimental method he influenced every branch of the science. For all of the zoölogical sciences today employ experiment as an important mode of investigation.

The Microscope.—Early biologists could concern themselves only with objects of some size, for microscopes were not yet in existence.

FIG. 5.—Marcello Malpighi, 1628-1694. (*From Garrison's History of Medicine, after the painting by Tabor, Royal Society.*)

Although the refractive power of glass with curved surfaces was known several centuries before the Christian era, the magnifying power of such glasses was not appreciated until long afterwards, and spectacles for the aid of vision are not mentioned until quite late in the thirteenth century. From such simple lenses came the microscope. The invention of the compound microscope is generally attributed to Zacharias Jensen, son of a Dutch spectacle-maker, who, about 1591 or soon thereafter, placed two lenses some distance apart in a tube and obtained clear images with them. The improvement of this first simple instrument has been the work of many persons since that time. In the absence of optical manufacturers, the scholars who needed microscopes made their own. Under these

circumstances, the development of the microscope could not be rapid. The instrument shown in Fig. 4 is the product of probably a century and a half of this slow progress.

Among the early designers and users of microscopes are to be mentioned Hooke and Grew of England, Malpighi of Italy, and Swammerdam and Leeuwenhoek of Holland, all of whom flourished in the latter half of the seventeenth or early eighteenth century. Hooke was too versatile to be remembered much in zoölogy, except in connection with the development of the microscope and the incidental discovery of cells in cork. Grew did some good work in the anatomy of plants. The remaining

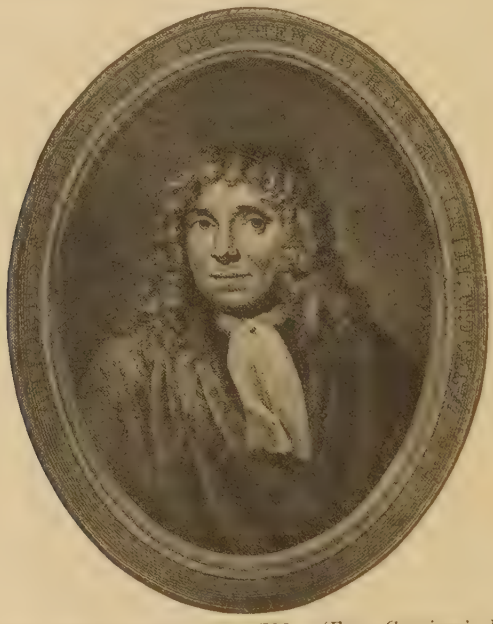

Fig. 6.—Antony van Leeuwenhoek, 1632–1723. (*From Garrison's History of Medicine.*)

three microscopists just named were much more productive in the strictly biological field.

Malpighi (Fig. 5) is famous for a treatise on the minute structure of the silkworm; for the discovery of the layer of cells at the base of the epidermis, which bears his name; for observations on the anatomy of plants; and for work in embryology. Swammerdam is known for his minute dissections of insects, snails, and clams. Leeuwenhoek (Fig. 6) studied blood capillaries, and the structure of muscles, and, together with a young physician, was one of the first to see and figure spermatozoa (the male germ cells).

Although the microscopes of the seventeenth century were not powerful, compared with microscopes of today, they opened up a large field

for new discovery. Minute anatomy had its rise with the rise of the microscope. It is not important to name the many investigators who, with the aid of these instruments, studied the systems of minute organs in insects, or who discovered the small one-celled animals in pond water. No one of them stands out preëminently as a representative of this movement. It will be sufficient to point out that the steady improvement of the microscope in the two centuries and more since the time of Malpighi and his contemporaries has made it possible to study more and more minute structures. Progress in anatomy, in so far as it concerns the smallest structures, has at all times depended on, and kept pace with, the improvement of the microscope. The physiologist must often watch his experiment with the aid of a good microscope. Classification of animals and plants in many cases shifted to an entirely new basis when observation of minute structures became possible. Microscopic study of fossils reveals features of importance. Naturally, each of these subjects has grown as the microscope grew. From an instrument like that illustrated in Fig. 4, which is by no means the crudest one known, the microscope evolved step by step to the splendid optical aids of the present time. Today the biologist uses microscopes fitted with oil immersion objectives and condensers for increasing the illumination, lenses corrected for chromatic and spherical aberration, devices for delicate adjustments of focus, and other refinements. Whether further striking improvements are still possible is uncertain.

Classification.—During all these centuries of observation, in the early Greek period and in the period following Vesalius, many kinds of animals came to be known. With the use of the microscope, hundreds more became visible. For a long time knowledge of these thousands of species was in a chaotic state, and with the improvement of the methods of study, and the increase in the number of travelers and naturalists, the number of known animals made the chaos intolerable. Systems of classification were used, but they were superficial and were devised for convenience only. It is true, even the early zoölogists knew that the quadrupeds were more like one another than any of them were like snakes, but no one had a comprehensive system of classification that included the whole animal kingdom. Nor was this the whole difficulty. Animals were often not named, but were known by cumbersome descriptions. Animals that were common enough to have received names were differently named in different regions; and the same name was not infrequently applied in different localities to different animals.

Order has come out of this confusion largely through the initial efforts of Carl von Linné (or Linnæus as he is more commonly called), of Sweden, who lived from 1707 to 1778 (Fig. 7). Before his time John Ray, of England, had taken one important step, by limiting the meaning of the word "species" to something like its present significance. Linnæus went

further and gave each species a name which, being Latin, could be used the world over. The name of each species was a double one, the first name being that of the genus, the second that of the species itself. Thus, the common cowbird is named *Molothrus ater*. The generic name is always begun with a capital letter and at the present time all specific names (of animals) with a small letter. From the use of two names for each species, this system of naming is known as the Binomial System of Nomenclature.

Linnæus's great work, the "Systema Naturæ," contained the first noteworthy application of this system of naming, in the form of a catalog,

FIG. 7.—Carl von Linné (Carolus Linnæus), 1707–1778, in Lapland dress at the age of thirty. (*Courtesy of New York Botanical Garden.*)

methodically arranged. The species were grouped into orders, and the orders into classes. While these groupings have since been shown to be artificial, and new groupings have been substituted, the binomial system of names has been retained and many species still bear the names which Linnæus proposed for them. The changes introduced into the grouping of species since Linnæus's time are intended to express ideas of the relationship of the groups to each other. But without a preliminary discussion of evolution it will not be profitable to pursue this matter further.

The advantages of a comprehensive system of classification are obvious. Any kind of arrangement is better than none. Such an arrangement, applied to animals, is not only a convenient aid to the other branches of zoölogy; it actually raises problems which would otherwise scarcely be discovered. The development of even a slight

degree of order out of confusion always suggests the possibility of further generalization.

Comparative Anatomy.—The next great movement in zoölogical progress was the development of comparative anatomy. Descriptive anatomy dates back to the ancients. But as larger numbers of animals became known, and especially under the influence of the Linnæan classification which placed similar animals in the same orders, it was inevitable that anatomy should become strongly comparative. Even as early as 1555, Belon noted the close correspondence, "bone for bone," between the skeleton of a bird and that of man. By 1645 there was published by Severino, a book expressly devoted to comparative anatomy.

FIG. 8.—Georges Cuvier, 1769–1832. (*From Locy's Biology and Its Makers.*)

Vicq d'Azyr, of France, who died at the early age of forty-six, made a brilliant beginning by comparing the arms and legs and brain of man with the corresponding structures in other animals.

The real founder of comparative anatomy was Georges Cuvier (Fig 8), a Frenchman (1769–1832). Not content to limit his observations to the vertebrates (backboned animals) as the earlier comparative anatomists were inclined to do, Cuvier made comparative studies through the whole animal kingdom. From 1801 to 1805 he published a systematic treatise on comparative anatomy, which included both invertebrates and vertebrates. A few years later he published a great work on fossil bones of the region about Paris, which was also comparative. From all these comparative studies Cuvier came to the conclusion that animals are built in accordance with four general types, the vertebrate type, the

molluscan type, the articulated type, and the radial type. He thus arrived at a scheme of classification based upon similarity of structure, which is even today the chief basis of classification. But curiously enough, Cuvier failed to see what every zoölogist now recognizes, that similarity of structure is owing to common descent. He even used his great powers of debate and his wide personal influence to combat the idea of common descent. The general acceptance of the idea of evolution was delayed many years by this error of Cuvier.

Following Cuvier was a long line of able anatomists in the nineteenth century, by whom comparative anatomy was raised almost to the rank

FIG. 9.—Theodor Schwann, 1810–1882. (*From Garrison's History of Medicine.*)

FIG. 10.—Johannes Evangelista Purkinje, 1787–1869. (*From Garrison's History of Medicine, W. B. Saunders Co.*)

of an exact science. Their names are everyday words to the trained morphologist, but no one of them stands forth preëminently, and they need not be mentioned here. The later ones recognized common descent as the key to similarity of structure, and comparative anatomy furnished some of the best of the early evidence of evolution.

The Discovery of Cells.—Early in the nineteenth century, before the end of Cuvier's career, the improvement of the microscope had resulted in such excellence that the study of the minute anatomy of animals and plants was becoming common among biologists. A number of investigators, some of them much earlier than the nineteenth century, saw in organisms minute divisions, arranged sometimes in orderly manner, sometimes in more random fashion. Hooke saw box-like cavities in cork as early as 1665, Malpighi a similar pattern in other plant tissues in 1670.

Oken claimed to have witnessed "repeated vesicles" in animals and plants, in 1808, but his statements are very vague. About the same time Lamarck and Mirbel described plants and animals as being composed everywhere of "cellular tissue," a fact that had for many years been taught by the former author to his students, but though at times Lamarck seems to have recognized that the important part of this tissue is "gelatinous," he had not observed nuclei, so that the idea of the individuality of cells did not take form. Ideas concerning the nucleus developed gradually, and this structure was recognized in 1833 by Brown as being of general occurrence in plants. Schleiden verified this conclusion as to plants, and Schwann (Fig. 9) extended it to animals. The nucleus afforded a criterion by which the existence of cells could be judged and the conception of cells as individual units of structure was firmly established.

The universal occurrence of cells in living things was recognized by Dutrochet and by Purkinje (Fig. 10). The latter sometimes called them cells, though more frequently globules or granules. The formal enunciation of the cell theory by Schwann in 1839, although based on his own studies, appears to have been a restatement of what was already well known to others. The credit for this great advance thus belongs to no one person.

The importance of the cell doctrine can scarcely be overestimated. It is taken as a matter of course, by beginning students, that all organisms are made up of cells; but when one reflects that all the things an animal is or does are what the cells are or do, the idea acquires tremendous significance. All growth, all development, all life processes, all reproduction, as will be pointed out in later chapters, are the results of cell activities. The universal occurrence of cells in organisms is, then, a fact of fundamental import.

Evolution.—While, on the morphological and purely observational side of biology, the cell theory was being built upon firm foundations, on the philosophical side new ideas were growing up which also marked progress in a different direction. Most zoölogists had become so well acquainted with animals as we know them at the present time that they conceived the various species to be fixed and constant. They believed each species to have been created in the form in which it now exists. Through a long period of biological history, however, there had not been wanting daring and inquiring naturalists who saw what they believed were indications that species had changed in the past, and were perhaps changing even at the present time. Vague ideas of evolution were held by some philosophers as early as the Greek period; but it was not until the end of the eighteenth century that any well-defined theory of evolution arose. Buffon (1707–1788) appears to have held evolutionary ideas, but was too timid to state them clearly. Erasmus Darwin (1731–

1802) published in his "Zoönomia" in 1794 a comprehensive theory of evolution, but did not support his views by many facts.

Lamarck (Fig. 11), 1744–1829, was the first to bring forward a theory of evolution that has retained a considerable following to the present time. Lamarck, like most of his contemporaries and predecessors, at first adopted the view that species were fixed and unchanging; but about 1800 his views changed. His theory is best explained in his "Philosophie Zoölogique," published in 1809. Its two principal tenets were that the effects of use and disuse upon the parts of animals are transmitted to their offspring, and that changes produced in animals by the environment

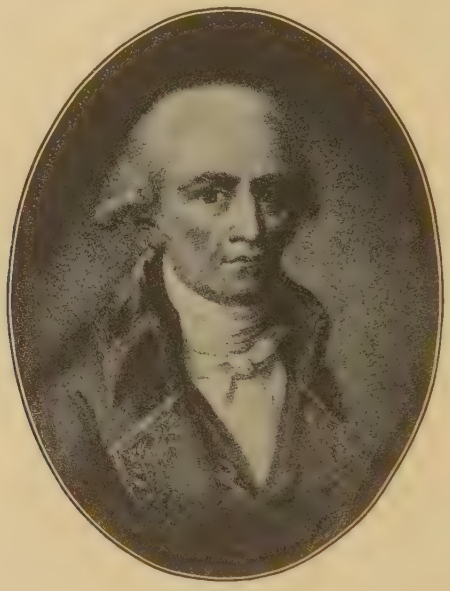

Fig. 11.—Jean Baptiste Lamarck, 1744–1829. (*From Locy's Biology and Its Makers and Thornton's British Plants.*)

are inherited by their progeny. Both of these views regarding the cause of evolution have been largely abandoned by the pure biologists, but are still held by some paleontologists, by numerous medical men, and by the laity.

Lamarck's views were championed by the able naturalist Geoffroy-Saint-Hilaire (1772–1844). Cuvier, on the contrary, not only opposed the Lamarckian views of the cause of change, but ridiculed the idea of evolution itself. The attitude of the latter scholar is one of the incongruities of biological history, since Cuvier's own discoveries in the field of comparative anatomy constitute one of the best arguments in favor of the theory of evolution. Nevertheless, Cuvier adhered to the fixity of species, and in a famous debate in the French Academy of Science between Cuvier and Geoffroy-Saint-Hilaire, in 1830, the former was held to have

won. Cuvier was in high esteem in government and social circles, and had a large following among the young men. As a result the rise of evolutionary thought was retarded for several decades.

Then came Charles Darwin (Fig. 12), grandson of Erasmus Darwin, with indisputable evidence of evolution. Cuvier was no longer living to combat the theory, and Darwin had laboriously collected a mass of supporting facts which could not be set aside. These he published in a series of books beginning with "Origin of Species" in 1859, and continuing to the end of his life in 1882. With them he proposed several theories to account for evolution which appeared so plausible that the

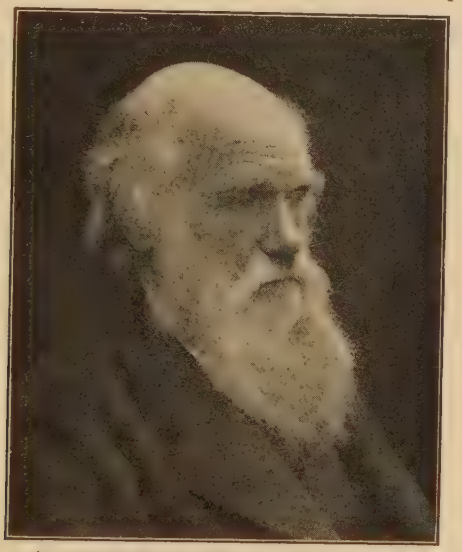

FIG. 12.—Charles Darwin, 1809–1882. (*From University Magazine. Photograph by Leonard Darwin.*)

whole thinking world was convinced of the fact of the mutability of species. The chief of these theories was that of *natural selection*, according to which, in the struggle for existence, the fittest survive. The theory of natural selection, as will be pointed out later, is still commonly held, though with diminished significance.

The doctrine of evolution was not accepted without opposition. However, with the aid of the powerful Thomas Huxley (Fig. 13), who spread the idea in forceful lectures among biologists and non-biologists alike, its victory was complete. With regard to the *fact* of evolution there are now no dissenters among thinking people. Whatever controversy still exists is concerned with the *causes* and *methods* of evolution; evolution is admitted by all.

Genetics.—It will be noted that the theory of natural selection, by means of which Darwin sought to explain evolution, contained nothing

to account for the *origin* of changes in species, but only for their *preservation*. So strongly did the theory of evolution and the theory of natural selection appeal to the imagination that another field of investigation, which would no doubt have gone far toward explaining evolution, was overlooked for a third of a century. This was the branch of biology now known as genetics, which includes heredity, variation, and related subjects.

A brilliant start was made in this field in 1866, by an Austrian monk, Gregor Mendel (Fig. 14). Mendel raised peas in the monastery garden, crossed a number of distinct varieties, and derived from them a simple

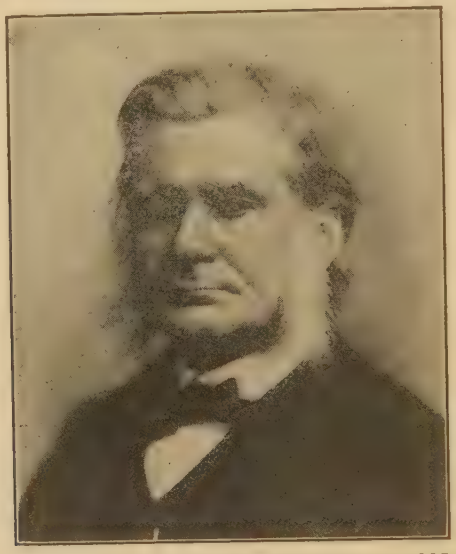

Fig. 13.—Thomas Henry Huxley, 1825–1895.

law of heredity. So occupied were biologists with Darwin's theory of evolution, then in its infancy that Mendel's writings remained unnoticed until 1900, when they were rediscovered. His simple experiments proved a tremendous stimulus to investigation, and much of the leading biological work of the present century has been in the field of genetics. Mendel's law of heredity has been amply verified and extended but at the same time modified. At the present time the best work in genetics is being directed toward discovering the details of the mechanism by which hereditary traits are transmitted from parent to offspring. When that is finally discovered, it is not improbable that the causes of evolution will be more clearly understood.

Applied Biology.—Although the foregoing account indicates the principal movements in the development of zoölogy, and the outstanding names connected with these movements, the pure science alone has been considered. It should not be forgotten that zoölogy has always

had its practical applications. In the last half century these applications have been greatly multiplied. Medicine is applied zoölogy, applied directly to man and incidentally to those animals that are parasitic upon him or that are carriers of disease. Sanitation and public hygiene are matters of applied biology even more than matters of engineering. Crop-destroying insects and other pests are combated by the economic zoölogist. Improvement of breeds of domestic animals is the practical aim of the student of animal husbandry. The applications of zoölogy to practical ends are still probably in their beginnings. Its applications to man himself are particularly in a backward state. The improvement

FIG. 14.—Gregor Johann Mendel, 1822–1884. (*From a photograph taken about* 1880. *Reproduced from the report of the Royal Horticultural Society Conference on Genetics*, 1906. *By permission of the President and Council.*)

of human qualities, the maintenance of the best human strains, the effects of migration and intermarriage upon the races of men and their political development, and the effects of war upon racial qualities, are problems which still await solution.

Appraisal.—Although zoölogy has had its fashions, though it has been developed in different directions at different times, these well-marked movements do not all bear the same relation to each other. The announcement of the cell theory stands in a peculiarly significant position. In itself the discovery of cells was not more important than some of the other developments of zoölogy. But it had and has unique possibilities as the foundation of other branches of the science. That animals are made up of cells is a purely morphological fact. But their physiology is

what it is because of the nature of cells. Inheritance and evolution are cell phenomena. Relation to environment is dependent on the functions of cells. Even geographical distribution and classification are fundamentally dependent upon the cellular characteristics of animals. As a preface, then, to the discussion of the various branches of zoölogy in later chapters, a knowledge of cells is essential, and to that subject attention is now turned.

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CHAPTER II

MORPHOLOGY OF THE CELL

According to the cell theory, as originally stated, though now recognized as incomplete, all living things, whether animals or plants, are composed of cells. As was to be expected, the theory contained some errors, at least in details. Its founders thought of the cell wall as the important feature. They had seen the nucleus within the enclosure formed by the walls, but regarded it as being in the wall. Moreover the nucleus was

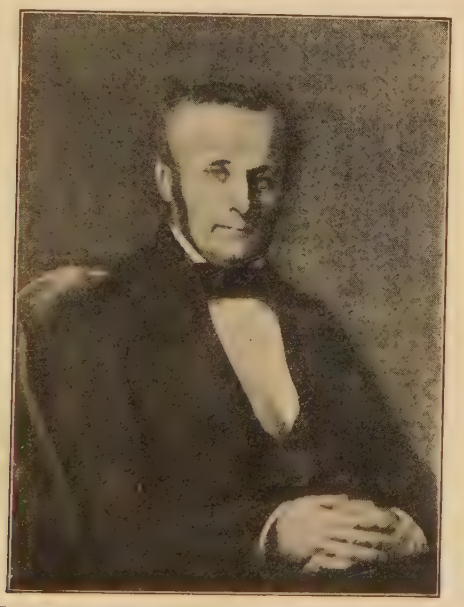

FIG. 15.—Felix Dujardin, 1801–1860. (*From Locy's Biology and Its Makers.*)

conceived to be the beginning of a new cell. Although the *protoplasm*, the living matter of which the cell is now known to be composed, had been seen by several investigators, none of them regarded it as the essential part of organisms. Schleiden called it by the common name gum. Dujardin (Fig. 15), a French naturalist, appears to have thought it worthy of more attention, and described it in 1835 under the name "sarcode" (soft substance). He tested its solubility, and its behavior with certain reagents, such as alcohol and the acids, thereby satisfying himself that it differed from other jelly-like substances (gelatin, albumen,

etc.) with which it might be confused. But either because Dujardin had studied the sarcode only in worms and protozoa and a few other low forms of animal life, or because his diffidence forbade his making any larger claim for it, this substance was supposed to be found only in the lower animals. The general occurrence of this substance, however, could not long avoid discovery. Hugo von Mohl, in 1846, observed the living part of plant cells, distinguishing it from the walls and vacuoles, and called it "protoplasm." This name, used earlier by Purkinje, von Mohl succeeded in bringing into common use. Gradually it dawned upon biologists that this matter is found in all living things, that it is in fundamental respects alike in all of them, and that this, rather than the walls,

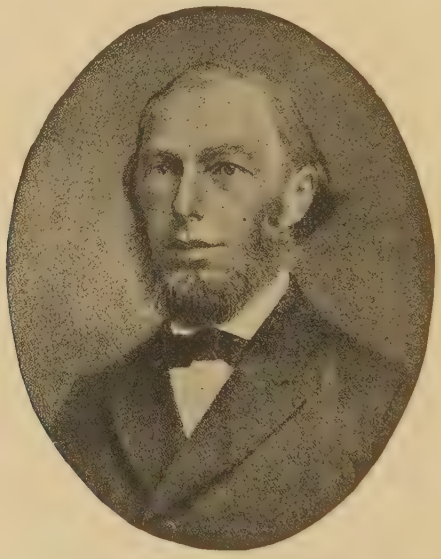

FIG. 16.—Max Schultze, 1825–1874. (*From Garrison's History of Medicine.*)

is the important feature of cells. In the absence of cell walls, this protoplasm is the cell. Of a number of investigators who contributed to this fortunate issue of the problem of the cell, mention should be made of Max Schultze (Fig. 16) who, probably more than any other one person, brought conviction of the truth of the idea just stated to the minds of all biologists.

Additions.—The bare statement that all living things are composed of cells is inadequate in at least one structural respect. It was early discovered that certain tissues are made up in part of structures and material that are not cellular, but that have been created by cells. The bulk of cartilage and bone is formed of a firm *matrix* not composed of cells, but lying between the cells. This matrix is produced by the cells as a secretion, in which the producing cells become imbedded. It is not changeless, since the cells may dissolve it away and build it in some other

direction, but it is itself wholly inactive in this change. The matrix is not living matter. Connective tissue also contains elastic matter, in the form of fibers of several kinds, which are laid down as secretions by the cells. These fibers have a function, but it is entirely a passive one. Ligaments and tendons are in like manner largely non-cellular. Since animal bodies are so largely composed of such non-living material, all of it produced by cells, the cell doctrine should specify that all living things are composed of cells *and cell products.*

With the corrections regarding the nature of nucleus, walls, and protoplasm, and the addition of cell products, noted in the preceding paragraphs, the early statement of the cell doctrine would still be essentially correct as far as it goes. In that form, however, it would imply that biology is mostly a morphological subject. So it once was. But with the growth of the science, with its development in the fields of physiology and genetics, it becomes apparent that the cell doctrine can be extended to include more than the mere structure of animals and plants.

The life processes of living beings, fortunately now fairly well understood in some respects, have been shown more and more to be the life processes of their component cells. Without implying that the cells act independently of one another, it is still in a sense true that the activities of an organism are the sum of activities of its cells. Under favorable cultural conditions, cells may long continue their activities when removed from their association with other cells; and in many cases it has been possible to analyze the complicated processes of multicellular organs, and show that this thing is done by certain cells, that other thing by certain other cells, and so on. The cell has now come to be regarded as the *physiological unit*, as well as the morphological one; and some of the most important advances in zoölogical knowledge in recent years have been made in the field of cell physiology.

Almost as a part of the step by which the cell doctrine is extended to embrace cell physiology as one of its tenets, is the inclusion of development and heredity. The origin of a multicellular animal from a one-celled beginning (the egg) may be watched from first to last, and everywhere the process is a series of cell phenomena. Cell divisions, arrangement of cells into layers or tissues, the unequal growth of cells or parts of cells to form folds and protrusions, the migration of cells sometimes for long distances, the formation here and there of cell products, make up the complex process of *embryonic development.* All these changes are brought about *in or by the cells.*

Through this series of multiple changes there is built up an organism which, in most cases, closely resembles its parents. Here again it is found that the cells are responsible for each step and for the final result. The complete heritage of the eventual adult animal must of course be represented in some manner in the egg. The proper distribution of the

material of heredity, whatever it is, through all of the divisions and rearrangements which the embryo undergoes, is at every point cared for *by the structure and functioning of cells*. What these structures and activities are need not be stated here, but they are dealt with in subsequent chapters.

An adequate statement of the cell doctrine, as must be apparent from the foregoing considerations, must do more than generalize upon the structure of living beings. It must include the fact that the cell is also the unit in physiological processes, including those of embryonic development and inheritance.

Influence of the Cell Theory.—The theory of the universality of cells was a great generalization. It would have been a most important milestone in biological progress, even if it had been in itself less fundamental. For zoölogy had had no great generalizations before the cell theory was brought forth. There was nothing in the field of biology to compare with Newton's laws of motion in physics. Biologists would have been pardoned for despairing of ever bringing the whole living world under one point of view in some specific regard. The cell theory, therefore, was a great unifying influence. Contemplation of it must have prepared biologists for other great generalizations. Less than half a century later, another fundamental proposition, the theory of evolution, had been accepted by practically the whole biological world; and it is not improbable that the idea of evolution was adopted the more readily because the cell theory had shown that basic unity was as much to be expected among living things as in physics and chemistry.

The knowledge that animals and plants are universally constructed of cells led to new problems. Comparative morphology could now extend its principles to an unsuspected host of minute structures. All the components of cells, including those of the nuclei and specialized organs, which are mentioned in the description of a typical cell below, have been discovered since Schwann's time; and the occurrence of these in cells of widely different kinds courted comparisons. Physiology now became the physiology of cells, or was capable of such extension. General physiology, as distinct from the physiology of the organs of higher animals, has grown out of this discovery. A knowledge of the permeability of cell membranes, of the functions of electrolytes in living substance, of the release of energy by chemical reactions within the cells, are some of the products of this new physiology made possible by the cell theory. Heredity could now become a cell problem, and as is pointed out in a later chapter the chief discussion of heredity now has to do with the machinery by means of which cells develop hereditary characteristics. Not all of these developments of zoölogical investigation took place at once, after the cell theory was published, but they became possible, and a beginning was made. But in order to understand the influence of the cell theory

on the development of the science, it will first be necessary to consider the structure of cells.

The Size of Cells.—All cells are composed of viscous or jelly-like material called "protoplasm." The quantity of this material comprised in a single cell varies within wide limits. Many cells are so small as to be visible only with a good microscope. The vast majority of cells require considerable magnification to be seen. Not a few, however, are large enough to be visible with the unaided eye as in the case of the larger protozoa (animals composed of but one cell), while in muscles and nerves of the higher animals, the cells, though not of great diameter, may be inches or feet in length. This great variability does not exist, however, among cells of the same kind. The cells of the skin of a given animal, though not of uniform size, do not differ strikingly from one another; and cells that are arranged in definite layers, like that lining the intestine, are apt to be very nearly equal in size.

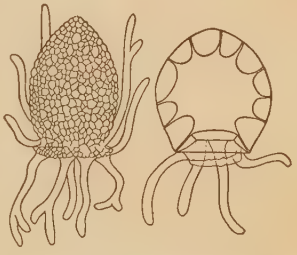

FIG. 17.—Two protozoa of the class Rhizopoda. The bodies are partly enclosed in shells, one made of sand, one of a chitinous substance. From these shells the protoplasmic body may be actively protruded in arm-like pseudopodia, which are afterwards retracted.

Gross Shape.—The shape of cells is also very variable. Theoretically, due to surface tension, a cell is typically spherical; but that shape is attained, even approximately, only in certain free cells, such as eggs and a few of the one-celled organisms, the protozoa (animals) and protophyta (plants). Cells take on other forms for various reasons. A free-living cell, as Amœba and other related protozoa, may actively change its shape by thrusting out portions of the body into finger-like pseudopodia (Fig. 17). Such an animal is seldom of the same shape for any considerable time (unless it goes into a "resting" state in which it is apt to be nearly spherical) and it may even be changing every instant. Other free-living cells, of more or less constant form, are kept constant by a wall or pellicle that the cells themselves have secreted. These pellicles may be flexible but firm, so that while the shape of the body may become temporarily distorted it is characteristic of the species. Good examples of such constant forms are found among the ciliated protozoa, as in Fig. 18.

Cells that exist in groups usually have their form altered by the mechanical pressure of the cells around them. When this pressure is the only factor altering their shapes, the cells are irregular polyhedrons. Other factors, such as unequal growth in different directions, and perhaps inequalities of surface tension, factors often not understood, combine to produce cells of a great variety of shapes. They may be rather regular rectahedrons, as in plants; long cylinders, as in voluntary muscle;

greatly flattened cells with their largest sides polygons, as in the outer layer of frog skin; somewhat flattened elliptical cells, as in the blood of many animals; circular and flattened or cup-shaped, as in human blood; narrow and spindle-shaped, as in involuntary muscle; or finely branched, as in pigment cells of the skin of frogs and salamanders, or bone and nerve cells.

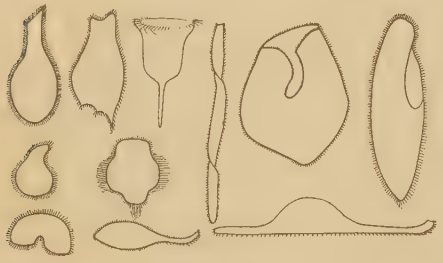

Fig. 18.

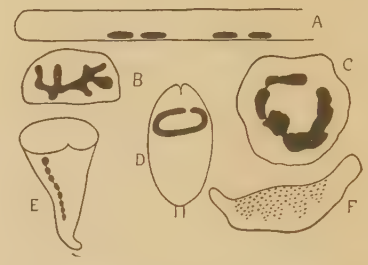

Fig. 19.

Fig. 18.—Various forms of ciliated protozoa whose body shape is kept fairly constant by a surrounding pellicle. Though this shape may be altered by pressure, it is restored when the pressure is removed. Cilia project from the surface. (*Modified from Conn.*)

Fig. 19.—Various forms of nuclei in cells. *A*, part of muscle cell with multiple ellipsoidal nuclei; *B*, gland cell of butterfly with branching nucleus; *C*, marrow cell of rabbit with ring-nucleus; *D*, Epistylis with curved rod-like nucleus; *E*, Stentor with beaded nucleus; *F*, Trachelocerca with distributed nucleus. (*B*, *C*, *F*, *after Wilson. Courtesy of The Macmillan Company.*)

Nucleus and Cytoplasm.—This mass of protoplasm, regardless of its shape and other modifications, is usually differentiated into two distinct parts. There is a central body called the *nucleus* (Fig. 20, *n*) which, in prepared and stained material, is usually highly stained, since it is composed of substances which have a high affinity for most of the common dyes; but in living material the nucleus is somewhat transparent, nearly colorless, and highly refractive like a lens. The remainder of the cell, outside the nucleus, is called *cytoplasm* (Fig. 20, *cy*). Both nucleus and cytoplasm are composed of protoplasm.

The nucleus is typically spherical, owing, as in the case of the cell as a whole, to surface tension. But this shape is often altered by the shape of the containing cell, by physiological activity of the nucleus itself, or for reasons not yet understood. In long narrow cells the nucleus is apt to be ovoid or ellipsoidal, as in young voluntary muscle cells (Fig. 19, *A*). In highly active cells it may be branched (*B*) or otherwise irregular (ring-shaped, *C*). In some of the protozoa it is rope-like (*D*), or beaded (*E*). There may be more than one nucleus, as in a number of protozoa, and in voluntary muscle (*A*). Some cells have no nucleus of the usual structure, but possess the deeply staining nuclear material in the form of scattered granules. The bacteria and some of the protozoa (*F*) are examples of this condition.

In the red cells of human blood the nucleus is actually wanting, although in their developmental stages they possess nuclei which later disappear.

The form of the cytoplasmic mass is of course the form of the cell as a whole, as described above.

Other Bodies in the Cell.—As indicated in Fig. 20, a cell may possess other features. There is a differentiated portion at the surface, whose nature is different in different cases, and which is variously designated. Often it is a lifeless secretion of the protoplasm, or *cell wall*, composed of various substances. Instead of a wall the surface of the cell may be covered with a thin, filmy sheet, called the *pellicle* or *cuticle* the nature

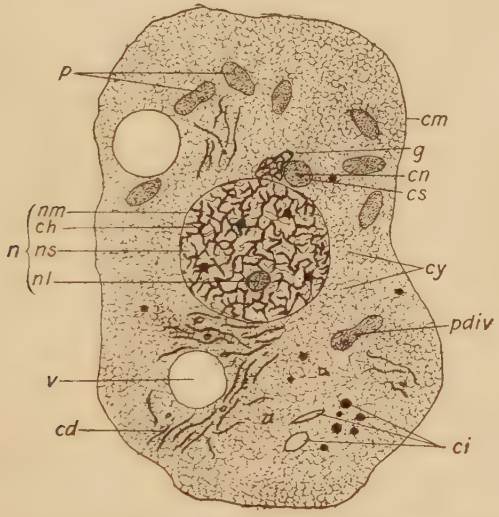

FIG. 20.—Diagram of a typical cell, with structures commonly present. *cd*, mitochondria; *ch*, chromatin network; *ci*, cell inclusions; *cm*, cell membrane; *cn*, centriole; *cs*, centrosphere; *cy*, cytoplasm; *g*, Golgi apparatus; *n*, nucleus; *nl*, nucleolus; *nm*, nuclear membrane; *ns*, nuclear sap; *p*, plastids; *pdiv*, plastid dividing; *v*, vacuole.

of which is uncertain. Probably the pellicle is to be regarded as a lifeless secretion, as is the cell wall. Such pellicles are found in the ciliated protozoa as described above (Fig. 18).

Whether naked or covered by a cell wall, the surface layer of protoplasm is differentiated, at least with regard to its physical and probably also its chemical properties. Depending upon their effect upon surface tension, certain substances tend to collect more at the surface than do other things, thus making the composition of the surface layer differ from that of the deeper-lying protoplasm. Surface tension also tends to force the larger globules contained in the protoplasm away from the surface, leaving only the smaller ones in the peripheral layer. For these reasons, a

very thin surface layer of protoplasm has a different composition and consistency, and is known as the *cell membrane* (Fig. 20, *cm*); but this membrane is not a secretion, it is part of the living matter itself. The term cell membrane is used, however, for other structures, some of which may be lifeless.

Plastids are not uncommon structures in cells (Fig. 20, *p*). In the higher plants they are universal, and they are usually green, though some are of other colors, giving color to certain fruits and flowers, and some are colorless. In animals, plastids are not uncommon in certain classes of protozoa where they are mostly colored.

Vacuoles are vesicles of liquid enclosed in the protoplasm. They may be permanent or temporary. In the protozoa, temporary vacuoles are common. They usually either enclose bodies of food in process of digestion, in which case they are called *food vacuoles*, or they disappear at intervals by ejecting their liquid contents through the surface layer of protoplasm into the surrounding medium. The latter kind is called a *pulsating* or *contractile vacuole* (see Fig. 20, *v*). In some cells a *centrosphere* (Fig. 20, *cs*) is found, usually near the nucleus. It is a mass of somewhat differentiated protoplasm, containing a minute body that stains deeply, the *centriole*. The centriole is sometimes called a "centrosome," while the latter name has also been applied to the centriole and centrosphere together. When present the centrosphere takes a conspicuous though probably not important part in cell division, as described in another chapter.

Structures known as *mitochondria* (Fig. 20, *cd*) are found in many kinds of cells, perhaps in all cells. They are of various shapes, rods, threads, or granules, and occur almost anywhere in the cytoplasm. Only in recent years has the widespread occurrence of mitochondria been discovered because they are often composed of material which readily dissolves in the more common killing fluids used in preparing cells for microscopic study. Many conjectures regarding their function have been made, but little is definitely known regarding it. An object known as the *Golgi apparatus* (Fig. 20, *g*), of various forms, often a conspicuous network, occupies various positions, usually near the nucleus and in some cases characteristically near the centrosphere. The function of the Golgi apparatus is still unknown though there is some indication that it takes part in the process of secretion by gland cells, and in the formation of the tip of the male germ cell.

Besides all the above structures which serve, or may serve, some function in the cell, and which may therefore be regarded as cell organs, there are often lifeless matters enclosed in the protoplasm. These may be grains of starch, or oil or fat globules, which the cell has produced and which are stored as future food. Or the lifeless objects may be undigested remains of organisms taken as food, or even objects picked

up incidentally along with food or otherwise. These non-living objects may be spoken of as *cell inclusions* (*ci*).

Polarity.—The structures described above do not constitute all of the organization which cells are known to possess. There is another type of organization which is termed *polarity*. In many cells, one portion is destined to perform certain functions, another portion other functions, even when these portions are visibly alike. In a developing egg, one part will become the nervous system and associated sense organs, another part the digestive tract. In the ordinary course of development these parts are not interchangeable. This evident arrangement of parts, as evidenced by their future activities, is the phenomenon which is called polarity. A good example of polarity is found in the eggs of insects, in which one end of the egg, in some way different from the other end, always becomes the head. Cells bearing cilia (hair-like projections) on one end are polarized. So also are nerve cells, or their connections, since nerve impulses travel over them in only one direction. In some of these cases the polarity is visible, but before the structures indicating the polarity were developed there was presumably an invisible difference in the protoplasm. The nature of this organization is not known.

FIG. 21.—Cell bridges or strands of protoplasm connecting the cells, in human mesoderm. (*After Maurer, from Sharp's Introduction to Cytology. McGraw-Hill Book Company, Inc.*)

Structural Relation to Other Cells.—When cells are free-living and independent, as in the protozoa, they may have little or no influence upon one another. When they are aggregated into masses, as in the multicellular animals, there is always the possibility that each cell may be modified, and its activities guided, by the cells around it. Often such interdependence must follow merely from the diffusion of fluids from cell to cell, or from surface phenomena. In some cases, however, protoplasmic connections extend from one cell to another. These have been demonstrated in the skin of the salamander, are conspicuous in Volvox, and have been described for many kinds of animal cells (Fig. 21). In plants, cell bridges are usually present, the fine protoplasmic filaments passing through minute pores in the cell walls. This connection between cells opens up large possibilities of mutual influence.

Structure of the Nucleus.—The nucleus is bounded by a thin membrane, called the *nuclear membrane* (Fig. 20, *nm*), which is differentiated out of the general protoplasm. Its composition appears to be not always the same. Within this membrane the bulk of the nucleus

consists of a liquid, the *nuclear sap* (*ns*), probably with various substances in solution. Stretched through this fluid is, in most common cases, a network of fine, apparently branching filaments of a substance named *chromatin*. These filaments are of varying thickness. The thicker points stain deeply with most ordinary dyes, and conspicuous thickenings are called *net-knots;* elsewhere the threads stain but lightly. The deeply and faintly staining parts were formerly thought to be different substances, but are now regarded as phases of the same substance.

The chromatin is the most important constituent of the nucleus, and indeed of the whole cell. It determines to a large extent, as is shown in subsequent chapters, the nature and activities of the cell. It is not a uniform material, but is differentiated into a number of chemically different substances. These different components are arranged in definite order in small bodies or *chromomeres* distributed along the filaments, and mechanisms operate in the division of cells and in the origin of reproductive cells to maintain this order, or to change it only in limited fashion.

Some nuclei contain, in addition to the sap and the network of chromatin, a *nucleolus* (*nl*). Two or more nucleoli may be present. They are rounded bodies that stain readily, but in a manner different from the chromatin. Nucleoli are therefore not to be confused with net-knots, which are sometimes unwisely called nucleoli. The nature and function of the nucleolus, when it is present, are not understood. Some biologists have regarded it as a waste product; others have held it to be a reserve supply of materials used in cell division, since it disappears during that process; and it has been regarded as a reserve food supply for the nucleus.

Only Gross Structures Described.—Though some of the structures so far mentioned are very minute, they are nearly all gross as compared with the finer structure possessed by protoplasm. Some of this finer structure is visible with good microscopes, some is demonstrated by the ultramicroscope, and the rest is inferred from experimental results and from theoretical considerations. This minute structure is so intimately associated with the activities of protoplasm, that an account of it is deferred to the next chapter.

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CHAPTER III

PHYSIOLOGY OF CELLS

The more fundamental part of physiology includes only the general functions of protoplasm. It is with this type of physiology that the present chapter deals. The functions of organs, systems, and tissues are deferred to later chapters in connection with the morphology of these structures.

The Composition of Protoplasm.—Cell physiology depends primarily upon the chemical composition and physical structure of the material of which the cells are composed. Too great emphasis cannot be placed on the fact that protoplasm is not a chemical compound, the structure of which may be expressed by a chemical formula, but that it is an elaborate mixture of chemical compounds in water. Some of these compounds are soluble or partially soluble in water, others are insoluble, some are organic, others inorganic. When qualitative chemical analyses of samples of protoplasm are made the results are different from different samples. A bit of protoplasm large enough to analyze, from any source, always yields carbon, hydrogen, nitrogen, oxygen, phosphorus, sulphur, sodium, potassium, magnesium, calcium, iron, and chlorine. Additional elements that frequently occur in such analyses are aluminium, silicon, manganese, copper, fluorine, bromine, and iodine. Still other elements occur rarely in protoplasm. The above lists of elements really tell very little, however, concerning protoplasm, since they do not suggest the manner in which the elements are combined, and it is the compounds, not the elements, which occur in protoplasm that are of chief importance. These compounds in protoplasm are of a variety of kinds, conveniently discussed under the general headings of water, salts, and the organic compounds, proteins, carbohydrates, fats, lipoids, and enzymes.

Water.—Water is the most abundant constituent of protoplasm, making about 65 to 90 per cent of the total mass. Water is so common as to be largely taken for granted, and yet, perhaps, it is not too much to say that the properties and activities of protoplasm are quite as dependent upon the remarkable properties of water as upon the properties of any other of its constituents. Some of these properties of water are its high specific heat, its great solvent power, its ability to dissociate salts into ions, and its high surface tension. So important are the properties of water to the activities of protoplasm that life without water is inconceivable.

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Salts.—Protoplasm is never free from salts in aqueous solution. The common metallic salts found in protoplasm are those of sodium, potassium, magnesium, calcium, iron, and manganese. These occur as chlorides, carbonates, nitrates, sulphates, and phosphates. The most common salts are the chlorides of sodium and calcium. As in ordinary aqueous solutions the molecules of the salts which are diffused through protoplasm dissociate more or less into ions. Solutions containing ions are capable of conducting an electric current and are called *electrolytes*. The ions themselves carry electrical charges and thus give any system which contains them certain electrical properties.

The Proteins.—These are compounds of *amino acids*, substances in which the *amino* group NH_2 and the *carboxyl* radical COOH are always present. Thus protein always contains carbon, oxygen, hydrogen, and nitrogen, but there may also be combined with these elements phosphorus, iron, magnesium, sulphur, etc. Since there are about eighteen amino acids which are capable of a great variety of combinations among themselves and with other substances, the possible number of proteins is great. All proteins have huge molecules, composed of hundreds or even thousands of atoms, and the arrangement of these atoms is always complex. An empirical formula (which states merely the number of atoms of each of the elements present) for hemoglobin, a protein derived from the red blood corpuscles, is $C_{712}H_{1130}N_{214}O_{245}FeS_2$. Obviously for such complex molecules it is impossible to suggest a structural formula.

Proteins coagulate upon heating or upon the addition of acids, alcohol, or salts to form a firm clot which often is not soluble in water. The coagulum produced by neutral salts is soluble. Proteins have a large molecular weight, slow diffusibility, and high resistance to the passage of an electric current. Proteins burn with the release of considerable heat, and incomplete burning is accompanied by the production of a characteristic odor. The products of combustion are carbon dioxide, water, and certain nitrogenous compounds.

Carbohydrates.—These substances are composed of carbon, hydrogen, and oxygen, and no others. The hydrogen and oxygen atoms are characteristically present in the ratio of 2 to 1, as in water. From this latter fact comes the name carbohydrate, which implies that the substances are hydrates of carbon. Ordinary cane sugar ($C_{12}H_{22}O_{11}$), glucose ($C_6H_{12}O_6$), the various starches, the cellulose of which cell walls are composed and others are carbohydrates.

Some of these carbohydrates are soluble, others insoluble. The soluble ones, as the sugars and syrups, may exist in any part of the protoplasm, and may diffuse readily from one part of the cell to another, or from cell to cell. The insoluble carbohydrates are stored as solid particles in the liver and muscle cells, as glycogen (animal starch) or as starch grains in plant cells, or as cellulose in cell walls. Under the

action of certain enzymes, to be discussed later, the insoluble carbohydrates may be converted into soluble ones. Carbohydrates burn (oxidize) readily with the release of considerable heat and the liberation of carbon dioxide and water.

Fats.—The fats and oils are compounds of carbon, hydrogen, and oxygen, as are the carbohydrates; but oxygen is usually less abundant than in the starches and sugars. Chemically, the fats are compounds of glycerol and one or more fatty acids. The character of a fat is determined by the fatty acid or acids entering into the composition. Fats are greasy and they leave a grease spot on paper which does not evaporate. They are not soluble in water, and are not thus capable of diffusion through the general protoplasm, but are stored. Most cells contain small quantities of fat in the form of droplets, while in the larger animals connective tissue may be heavily laden with it. Good examples of fats are butter, lard, and tallow derived from animal sources and oils, such as olive, castor, and cocoanut oils derived from plants. Fats combine readily with oxygen when burned and yield much more heat than do the carbohydrates. Thus a gram of starch yields about 4.19 large calories, while a gram of fat yields about 9.3 large calories. The products of the combustion of fats are carbon dioxide and water.

Lipoids.—The term lipoids is applied loosely to a certain group of substances whose chemical and physical properties resemble those of fats. They are often sticky and waxy in consistency. Like the fats, they are insoluble in water and are soluble only in substances of low surface tension. The lecithins are some of the very common lipoids, found in quantity in the yolk of eggs; cholesterin is also usually included in this class of substances; and there are many others.

The structure of the lipoid molecule is simpler than that of proteins, and in many cases it is well understood. Although the lipoid molecules are large, containing often a hundred atoms, the empirical formulas of certain of them have been definitely determined. Moreover, their chemical relations are so well understood that there is no hesitation in ascribing to some of them definite structural formulas.

The principal elements in the lipoids are carbon, hydrogen, and oxygen; but phosphorus and nitrogen are often also present. On the whole they tend to lower the surface tension of cells, and may be found collected in larger quantities near the surface of the cell, forming part of the cell membrane.

Enzymes.—Enzymes are substances whose exact chemical nature is yet unknown. Extracted enzymes may apparently respond to protein tests, but this seems to be due to proteins associated with the enzymes, from which the latter have only occasionally been separated. Enzymes act like certain substances which have the property of hastening chemical reactions. These accelerating substances are called *cata-*

lysts and the effect which they have in the reaction is called *catalysis*. Among inorganic substances which act as catalysts may be mentioned finely divided platinum. At least some of the catalysts hasten reactions by entering into the formation of intermediate substances from which they are promptly released. They are thus present undiminished at the end of the reaction. Enzymes also act somewhat in this fashion. Unlike the inorganic catalysts, enzymes are affected by extremes of heat or cold. Most of them operate best at a temperature of 30 to 45°C. but are destroyed by temperatures of 60 to 75°C. A given enzyme may take part in only a single kind of reaction. This reaction, however, is reversible, that is, the enzyme may assist in the splitting of a substance into two others or it may serve as the agent for causing the combination of the two simple substances into the one. The limitation of an enzyme to a certain specific action is visualized by Fischer's famous "lock and key" hypothesis which assumes that the chemical configuration of the enzyme corresponds very closely to that of the substance on which it acts, and that the two are thus fitted to each other as a key is fitted to a lock. From the fact that many enzymes may take part in but one kind of reaction it may be inferred that to accomplish the multitude of chemical reactions that are going on continuously or periodically in the animal or plant a number of enzymes must be present in every living organism. A large number of enzymes have already been isolated and determined from plants and animals, and it is probable that many more will be found. An enzyme is named according to the substance upon which it acts or after the most important product of its action.

Diffusion.—Quite as important as the chemical composition of the substances in protoplasm are the physical properties of the mixture. One of the most important of these physical properties of protoplasm is the readiness with which it permits the passage of the molecules of certain other substances through it. The dispersion of the molecules of one substance into another is called *diffusion*. Thus, gas may diffuse into a gas or into a liquid, or a solid or liquid into a solid or liquid. The rate of diffusion of a gas into a gas is rapid, but the rate of diffusion of solids or liquids into a solid or liquid is slow, sometimes extremely slow. The mixtures resulting from the diffusion of solids into liquids or solids, or of liquids or gases into liquids, are known as *solutions*. If the process of diffusion is permitted to go on until an equilibrium is established, a homogeneous mixture results. When a solid is dissolved in a liquid the liquid is called the *solvent* and the solid the *solute*.

Osmosis.—As was said in the discussion of diffusion, miscible liquids diffuse into each other so that a homogeneous mixture is finally formed. If a semipermeable membrane, by which is meant one that is permeable to solvents but more or less impermeable to dissolved substances, be

interposed between water and a substance dissolved in water, it may be noted that the water passes through the membrane while the passage of the substance in solution occurs less readily, or not at all.[1] The passage of water or other substances through a membrane is known as *osmosis*. This term, as distinguished from diffusion, is especially applied when different substances pass through the membrane with unequal facility. Animal membranes, such as the tissue of the urinary bladder, often do not even approximate the characteristics of an ideal semipermeable membrane, yet they usually resist the passage of certain substances through them. If a piece of bladder is stretched over the open end of a funnel or thistle tube containing sugar solution, and the tube is inverted in a dish of pure water (Fig. 22) the water will pass through the membrane causing the solution to rise in the tube, and some of the sugar may pass through to the water of the dish. The rise of the solution in the tube creates in the tube a hydrostatic pressure which is known as *osmotic pressure*.

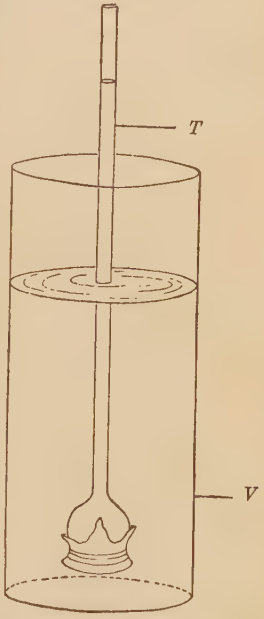

FIG. 22.—Diagram of apparatus used to illustrate osmosis. *T*, inverted thistle tube covered with animal membrane and containing a solution of sugar in water; *V*, vessel of water.

Osmosis, often in somewhat modified form, is an important feature of life processes. The turgidity of plant cells, and the size of cells of all sorts is dependent upon it. Because of osmosis the permeability of cell membranes is generally regarded as significant. In higher animals, as is pointed out in a later chapter, modified osmosis has much to do with the absorption of nutrient materials, and with the elimination of wastes in excretion.

Physical Structure of Protoplasm.—Protoplasm is not homogeneous, but is composed of many parts in complex relationship. In general, it consists of particles of various sizes, mostly very minute, distributed through a supporting liquid substance. In the terms of physical chemistry, protoplasm is a "system" consisting of two "phases," of which the particles are the "dispersed" phase and the supporting liquid the "continuous" phase. In so far as the dispersed particles are liquid and large enough to be visible in a microscope, such a mixture is an emulsion (Fig. 23). Where the particles are solid and of such visible size, it is a

[1] Ideally a semipermeable membrane does not permit the passage of dissolved substances at all. Since, however, an ideal semipermeable membrane probably does not exist, the term is loosely applied to membranes which greatly retard the passage of substances in solution and thus approximate the requirements of the definition.

suspension. If the particles are submicroscopic in size, the mixture is an emulsoid or a suspensoid according as the particles are liquid or solid. The existence of such invisible particles may be detected with the ultramicroscope, using oblique illumination against a dark background. Most protoplasm probably exists in all these states at the same time. In general, such a mixture is said to be colloidal. Even the fine particles are mostly larger than molecules, and so may be composed of more than one substance. Their composition cannot be precisely known, but they must be relatively insoluble in water in order to maintain themselves as particles. There are indications that the particles are surrounded by a lipoid film, which may have something to do with their insolubility in water.

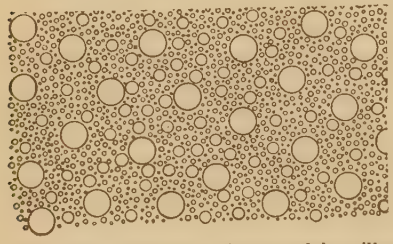

FIG. 23.—Diagram of an emulsion, illustrating the physical structure of a very common kind of protoplasm.

In addition to such particles, protoplasm always contains substances in true solution; that is, the dispersed (dissolved) particles are not larger than molecules, and these are small enough to have none of the characteristic properties of colloidal substances. The salts and the soluble carbohydrates are thus dissolved.

Surface Phenomena.—An important consequence of the protoplasmic structure just described is the enormous surface exposed by the dispersed particles to the continuous phase of the system. Extremely finely divided particles present a greater surface relative to their volume than do larger particles. This great surface increases the rate of physical and chemical activity at the interfaces, that is, at every face of contact between the two phases of the system. These activities which have their locus at the interface have been called *surface phenomena.* Some surface phenomena are surface tension, surface energy, adsorption, and various electrical phenomena. Protoplasm exibits these phenomena because of its colloidal structure.

Adsorption.—Adsorption is one of the remarkable and important phenomena of finely divided substances, whether solid or colloidal. Extremely finely divided solids or those with extremely fine pores tend to condense on their surfaces any gases or vapors or other substances with which they are in contact. The thin films of these adsorbed substances are held so tenaciously that great pressures are required for their removal. A gas mask removes gases from the air because of the great adsorptive power of charcoal, and the clarification of syrups and sugars is accomplished by making use of the adsorption of coloring matter by bone black. Certain properties of living matter are best explained on the basis of adsorption, as indicated later. It has been suggested by some that in

the red blood cells oxygen is held by the hemoglobin, not by chemical combination, as usually supposed, but by adsorption.

The fine particles of protoplasm, in general, are believed to adsorb ions of dissolved salts and hence to possess certain electrical properties. Some physiologists have thought that cell membranes are adsorption products, but that is probably not entirely true.

Electrical Properties.—The electrical properties conferred on protoplasm by ionized salts have been mentioned. Ions are capable, as in electrolytic cells, of conducting electricity, but in protoplasm are more important because they are probably adsorbed upon the surfaces of the colloidal particles. These particles thereby acquire an electric charge. Through the interior of a cell the particles appear to carry positive charges, but in the nuclear sap they are negative. The surface of a cell as a whole seems to be negatively charged. The occurrence of like charges on the interior colloidal particles, causing mutual repulsion, is probably the chief reason why these particles do not adhere to one another producing coagulation of the protoplasm.

Precipitation Reaction.—Protoplasm appears to be universally capable of producing membranes, not only on the surfaces of cells, but within the cells also. These membranes were long thought to be due to adsorption, in conformity with the so-called Gibbs-Thomson principle, according to which substances which have the capacity to lower surface tension tend to collect at surfaces. It is now suggested, however, that they are due to a precipitation reaction, caused by a definite substance in the protoplasm, in the presence of calcium or strontium, in somewhat the same manner as blood is coagulated. Such a reaction may occur in the interior of a cell, producing globules or vacuoles. The functions of membranes are various. The membranes determine very largely what substances may enter or leave cells, for this process is highly selective. An advancing pseudopodium of Amœba has a lower surface tension at its tip, due to some change in the membrane there. Whatever elasticity cells have is apparently due to membranes or to fibers like the astral rays (see the next chapter) which are probably also precipitation products. There is also some reason to believe that a coagulation, not unlike the precipitation that produces membranes and fibers, occurs in the protoplasm of muscle cells and is responsible for the contraction of the muscle.

Changes in Viscosity.—Probably closely related to this precipitation is the fact that the protoplasm may increase greatly in viscosity, then return to a more liquid state. Ordinarily the viscosity of the continuous phase or supporting liquid is only three or four times that of water, while with the dispersed particles included it is only eight or ten times that of water. The viscosity of the nuclear fluid is only twice that of water. Since glycerine has a viscosity a thousand times as great as water, it will be appreciated that protoplasm is really very fluid. As

suggested above, this fluid state is presumably maintained largely by the existence of like electric charges on the colloidal particles in the interior of the cell. However, the viscosity changes repeatedly. Such changes constitute part of the life of the protoplasm, and if they are prevented the protoplasm cannot function. Anesthesia involves a condition of unchanging viscosity, and if such constancy is permanent the protoplasm is dead. Cells bathed with a weak solution of ether have their viscosity lowered as long as the ether is present, while a strong solution coagulates them. Viscosity regularly changes during cell division, as described in the next chapter, being highest just before the formation of the spindle, and lower in all later stages. High viscosity, at least that which occurs in cell division, is not due to the formation of any network of fibers in the continuous liquid phase, nor to coalescence of the dispersed particles, but apparently to a precipitation occurring in the continuous phase, not unlike that described in the preceding section.

Diffusion in Colloids.—Solid emulsoids absorb much water, which causes them to swell enormously. Not all liquids are absorbed to the same degree. Thus gelatin imbibes much water, but very little alcohol. Many salts in solution diffuse readily into solid emulsoids, but others enter slowly or scarcely at all. Some salt solutions diffuse into gelatin at about the same rate as pure water. The solutions of various salts diffuse into protoplasm at widely different rates and the rate of diffusion of a given salt solution may vary with the kind of protoplasm. These facts have been variously interpreted. One interpretation is that the cell membrane has the power of changing its permeability, and another is that the colloids of the cell have different degrees of affinity for the ions of various salts.

Colloids in general do not diffuse readily through semipermeable membranes or through colloids. This statement applies to the colloids of cells as well as to other colloids. Possibly diffusion of colloids does not occur because the colloid particles are larger than the pores of the membrane, or because the colloid particles are adsorbed by the surfaces of the pores, and thus clog them.

Metabolism.—The protoplasm of the cell carries on all the general processes of the living body. Within the cell occurs a multitude of complex chemical reactions by which the protoplasm maintains and renews itself, and produces more protoplasm. Protoplasm digests food and for this process secretes various chemical substances. When food is broken down into simpler substances during digestion it is absorbed and built up into the living substances itself, or perhaps is combined with oxygen for the production of heat and motion. Protoplasm also respires, gets rid of waste materials by the process of excretion, grows, is capable of movement, and responds to changes in external conditions,

or exhibits irritability. The chemical processes involved in all these activities of protoplasm are included under the one term *metabolism.*

Metabolism may be defined as the sum of all the chemical and physical processes carried on within the organism. From the brief account of the activities of protoplasm outlined above it is obvious that metabolism may be divided into two phases, namely, the constructive phase or *anabolism* and the destructive phase or *catabolism.* Anabolism includes all the processes concerned in the growth and repair, or upbuilding, of protoplasm. It properly includes all processes of synthesis by which substances are transformed into reserves of food. Catabolism, on the contrary, includes all those processes opposed to anabolism. These are the processes by which protoplasm is broken down and the waste products eliminated. Both anabolism and catabolism are continuous processes. As long as anabolic processes are in excess of catabolic processes growth continues; but when catabolic processes are in excess a diminution in size takes place. Thus in progressive emaciation due to starvation or undernutrition catabolism is in excess of anabolism, reserves of food (carbohydrates and fats) are being consumed, and body weight decreases. Some of the aspects of metabolism barely touched upon in the foregoing discussion are considered further.

Intake and Preparation of Substances.—Animals are incapable of synthesizing the simple organic and inorganic compounds which occur in the water, soil and air about them. Plants, however, readily make complex organic substances from the raw materials about them, and they store in various parts of their bodies reserves of food stuffs which they can later use in their life processes. Animals make use of these stores by consuming the plants as food. From this food, and from water, salts, and oxygen otherwise obtained, the animals build up their bodies. In order to understand the nature of the foods utilized by animals it is first necessary to consider briefly the intake of materials in plants and the syntheses which go on in plant cells.

Intake in Plants.—Obviously plants can take into their cells only those substances which come into contact with them. These substances are the gases which exist in the air or are dissolved in water, the solids which exist in the soil and rocks, and water, in which some of the other substances may be dissolved. The elements taken into the plant may be ascertained by careful chemical analyses of plant cells. A number of such analyses show that plant bodies always contain carbon, hydrogen, oxygen, nitrogen, sulphur, phosphorus, potassium, magnesium, calcium, iron, sodium, chlorine, and silicon. In some plants there are also iodine, bromine, fluorine, and many other elements. Critical experiments have been instituted to determine the minimum chemical requirement for green plants. Plants are grown, for example, in water cultures containing known substances in solution. Green plants will not make

a normal development if any of the following elements are lacking: carbon, hydrogen, oxygen, nitrogen, sulphur, phosphorus, potassium, calcium, magnesium, and iron. Except oxygen, these elements are never used by green plants in their uncombined form, but as compounds. The carbon, except in plants that get material already elaborated by other organisms, is derived from the carbon dioxide of the air. Hydrogen and oxygen are utilized in the form of water, and oxygen is also secured uncombined from the air or from solution in water, and combined in many salts and oxides. Nitrogen is utilized by most plants in the form of nitrates. Lower plants, as fungi and certain algæ, and some of the carnivorous plants secure nitrogen in other forms. One of the chief sources of nitrogen is ammonia (NH_3) which is one of the products of the bacterial decomposition of organic material, that is, the bodies of plants or animals, or animal excrement. Ammonia is not, however, used as ammonia by green plants. The nitrogen of ammonia is made available to green plants through the action of certain bacteria which transform the ammonia into nitrites while other bacteria transform the nitrites into nitrates. As nitrates the nitrogen can be utilized by green plants. In addition to these bacteria certain other species of which Azotobacter is an example, are capable of fixing free nitrogen from the air, that is, of converting it into chemical compounds, and thus making it available for use, not only by these bacteria but also by green plants. Certain species of nitrogen-fixing bacteria live in symbiotic relation with leguminous plants, as beans and clover, forming nodules on their roots. These bacteria fix more nitrogen than they can use for themselves and this is available for the green plant. Sulphur is taken into the plants as sulphates; phosphorus in the form of phosphates; potassium, magnesium, calcium, iron and other elements in the form of various salts in solution.

The carbon dioxide, water, and salts are combined within plant cells to make more complex compounds and these may be further modified and combined. A plant cell is thus a laboratory or factory for the making of chemical transformations, most of which defy the chemist to duplicate.

Photosynthesis.—The best understood synthesis accomplished by plants is that which results in the formation of the carbohydrate glucose. This process is known as *photosynthesis*. Carbon is an essential part of all living matter. Its source for green plants is the carbon dioxide of the air, or for submerged plants the carbon dioxide dissolved in the water. The carbon dioxide is derived from the oxidation of organic matter. Carbon dioxide dissolved in water diffuses through the outer layer of protoplasm of the plant cell and is taken up by the chloroplasts, the green plastids of the cell. In these chloroplasts is a green substance known as *chlorophyll*, with two accompanying yellow substances *carotin* and *xanthophyll*, and several enzymes. The chloroplasts are

the factories in which the raw materials are transformed into glucose. The raw materials used are carbon dioxide and water, and the energy for the operation is derived from light. There can be no manufacture of glucose in the dark, nor without carbon dioxide and water, nor (with a few exceptions) in the absence of chlorophyll and enzymes. It has been shown that the red rays of the spectrum are most effective in the process, blue is next while the other colors have less effect.

The first substance that can be readily identified in photosynthesis is the end product glucose ($C_6H_{12}O_6$). Various suggestions have been offered for the intermediate steps which occur in the formation of glucose. One of these is that the carbon dioxide and water unite to form carbonic acid which is in some way reduced, perhaps to formic acid, and the formic acid is then reduced to formaldehyde. In this process oxygen is set free. Six molecules of formaldehyde then unite to form glucose. By the condensation of many molecules of glucose and the elimination of some water, the glucose is changed into starch which has the formula $(C_6H_{10}O_5)_n$. Glucose may be changed into other sugars, especially maltose ($C_{12}H_{22}O_{11}$), and the latter may be changed into starch. The sugars are soluble and in some plants, as sugar cane, may not be transformed into starch. Starch is insoluble and is temporarily stored in the form of starch grains in the chloroplasts. It is readily reconverted into a soluble carbohydrate (glucose) and in this form may be transported to other parts of the plant where again it may be converted into starch and stored in leucoplasts, or the glucose may be converted into cellulose, a form of carbohydrate used in cell walls. The transformations of glucose into other carbohydrates do not require chlorophyll nor light and are not part of the process of photosynthesis.

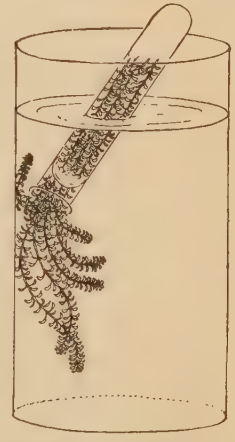

FIG. 24.—Method of collecting oxygen produced by the aquatic plant Elodea during photosynthesis. The oxygen rises from the plant into the closed end of the test tube.

The oxygen released in the process of photosynthesis may be readily recovered and tested, particularly if water plants are used for the experiment. In such an experiment the cut ends of a water plant, as Elodea, are inserted in a test tube filled with water, the plant and tube are immersed in water and then the tube is inverted (Fig. 24). When the plants are placed in sunlight bubbles of gas escape from their cut ends and collect in the tube. The usual tests show the gas to be oxygen.

Protein Synthesis.—Plants synthesize proteins from soluble carbohydrates and nitrates. This function is possessed by green plants and also by bacteria and molds. From the standpoint of the production of proteins which can be used as food by animals the activities of the green

plants are the only ones which are of importance. If animals possess the power of synthesizing proteins from fats or carbohydrates and ammonia they do so to only an exceedingly slight extent, and so are dependent upon plants for proteins.

In the synthesis of proteins plants make amino acids of many kinds. These are combined in various ways to form different kinds of proteins. Amino acids all possess one or more carboxyl groups of atoms (COOH) which give them their acidic properties, and one or more amino radicals (NH_2) which give them basic properties. A simple example of an amino acid is alanine, whose structural formula is

$$\begin{array}{l} CH_3 - CH - COOH \\ \quad\quad\quad\quad | \\ \quad\quad\quad\quad NH_2 \end{array}$$

About eighteen different amino acids have been derived from proteins, all capable, because of their NH_2 and COOH groups, of acting either as bases or as acids or as both at once. The amino acids readily combine with one another, the amino radical of one and the carboxyl group of another serving as the point of combination. In the union, water, taken partly from each amino acid molecule, is removed. The two molecules thus joined may be of the same amino acid, or of two different acids. Thus, from eighteen amino acids, a considerable number of new substances could be produced, even if the acids were combined only two at a time. The variety of combinations, however, is not thus limited, for several or many molecules may be joined, and each molecule may be of a different acid, or the various acids may be represented in different proportions, or the arrangement may vary. Furthermore, other substances than amino acids may be joined to the combined product at various points, so that the variety of substances that can conceivably be created wholly or chiefly of amino acids is almost unlimited. Add to this the fact that the arrangement of the molecules of the acids in the combined product may be different in different cases, owing to the fact that unions may often be made at any one of several points in the molecule, and the diversity of the possible aggregations is greatly multiplied. Other circumstances could be named which would lend still further emphasis to the fact that from a comparatively small number of amino acids an enormous number of compounds may be produced, but the diversity of possible amino compounds has already been sufficiently indicated.

From such combinations of amino acids and other substances all the proteins of plants and animals are constructed. This statement is not purely hypothesis, for the construction of *polypeptides*, as the compound substances described above are called, out of amino acids, and the careful decomposition of proteins, have been carried to a point at which they meet. The brilliant work of Fischer and others in the synthesis of

polypeptides has resulted in substances which are *identical* with substances that may be derived by the decomposition of natural proteins. Whether synthesis may ever be carried so far as to produce substances identical with the natural proteins themselves cannot be foretold; but already the synthetic work has yielded a large portion of the secret of protein structure. The importance of this revelation will become apparent in a later chapter when the digestion of the proteins is discussed. For in digestion, by a process the reverse of Fischer's synthesis, that is, by hydrolysis or the *addition* of water, the protein molecules are dissociated into their amino acid components.

As foods for animals those proteins are best which include in their molecules all of the amino acids. Many proteins produced by plants do not contain all the amino acids, and thus these do not meet the entire amino acid needs of the animal.

Synthesis of Fats.—Fats are synthesized in both plants and animals. Plants construct them from carbohydrates. They probably make *glycerol* (glycerine) from glucose, and from glucose or other carbohydrates they make *fatty acids*. Three molecules of fatty acids then combine with one molecule of glycerol to form one molecule of fat. As in proteins, a molecule of water is removed at each point of union. Plants make several kinds of fatty acids and molecules of one or more of them may enter into the formation of a fat molecule. Animals secure some of their fats directly from plants but before the fats can be utilized they must first be hydrolyzed into glycerol and fatty acids. These substances are absorbed and then recombined into fats. Animals also commonly synthesize fats from carbohydrates and to a certain extent from proteins, if proteins occur in excess in the diet. The principal fatty acids found in the fats of animal bodies are *stearic*, *palmitic*, and *oleic*. Since all of these may be present at the same time, one, two, or three kinds of fatty acids may unite with glycerol in the formation of a fat molecule.

Vitamins.—Important but only imperfectly understood components of a mammal's nutrition are the vitamins. Most of them have not yet been isolated, but their existence in certain articles of diet is inferred from the physiological consequences of such diet. In the absence of knowledge of their chemical nature, the vitamins have been designated A, B, C, D, and E. A mammal whose diet is deficient in vitamin A is subject to xerophthalmia, a dry and lusterless condition of the eyeball. Vitamin B is composed of two parts, of which one prevents polyneuritis, the other promotes growth. Vitamin C prevents scurvy, D prevents rickets, and E is necessary to the development of the fœtus in the uterus, being spoken of as the antisterility vitamin. Two of them are soluble in fats, existing in milk, butter, and other animal fats, but not abundantly in vegetable oils. Others are soluble in water, and are abundant in leafy vegetables, many fruits, and yeast. From these sources they are

obtained by animals, and since an excess of them is stored in several animal tissues, even carnivorous animals obtain the necessary supply of them. The surest way of including all the important vitamins is the use of a well-rounded diet. Since heat largely destroys some of the vitamins, raw foods (especially leafy vegetables) are usually advantageous when they can be used without great danger from disease-producing organisms.

The method by which vitamins operate to maintain health is not certainly known. The substance known as cholesterol was once thought to be vitamin D. Later it was discovered that a very similar substance, ergosterol, existed as an impurity in the cholesterol that was used, and that the antirachitic properties revealed by the latter substance were due to the ergosterol. Irradiating ergosterol with ultraviolet rays greatly augments its antirachitic effect, which suggests that the vitamins may act as storage media for radiant energy.

Digestion in Cells.—In unicellular animals digestion of necessity occurs within the cell. Food having been ingested comes to lie in vacuoles. Along with the food there is usually engulfed a small quantity of water. Into this water digestive solutions of acid or alkaline reaction are secreted by the surrounding protoplasm. These solutions contain enzymes, the nature of which may be inferred from the reaction of the solution. Obviously it would be quite impossible to secure a sufficient quantity of the digestive solutions of these minute animals to permit of analysis in the ordinary manner, but by making use of very dilute watery solutions of certain dyes as indicators, it is possible to determine the reaction of the digestive solutions in the living animals. The dye penetrates without killing the protoplasm, and the color changes may be observed in the vacuoles of the living animal by means of the microscope. The indicators do not directly distinguish the enzyme which is present. It is known, however, that some enzymes operate only in an acid medium and others only in an alkaline medium. Indicators therefore make possible certain inferences in regard to the kinds of enzymes which are secreted by these cells.

In plant cells carbohydrates, fats, or proteins are rendered soluble by the aid of digestive solutions containing enzymes resembling those found in animals. The foods may be in direct contact with the protoplasm or contained in vacuoles or plastids.

Digestion in higher animals is of two sorts, that which occurs within cavities of special digestive organs and that which occurs within the tissue cells of the body. Only the latter can be described here. The chief reserve food of animals is stored in specialized connective tissue cells which may be more or less scattered throughout the body, or localized, as in the so-called fat-bodies. In addition to this major reserve there is always a smaller supply of fat occurring as minute droplets in all tissue cells. Reserve carbohydrates occur in tissue cells, chiefly as granules

of *glycogen*, a material which has the same empirical formula as starch. Reserves of proteins are found in the protoplasm itself, or in an inactive form in special storage bodies. None of these foods can be used for the production of energy or for the upbuilding of protoplasm until it has undergone digestion, a process which must necessarily occur within the cell. This is accomplished by means of enzymes secreted by the protoplasm of the cells in which the reserve foods are being digested. Subsequent to digestion within the storage cells the products of digestion may be transported to other parts of the body, but the account of this transfer belongs in a later chapter.

Assimilation.—After foods have been rendered soluble and diffusible they are absorbed. Absorption occurs through the protoplasm adjacent to the vacuoles in protozoa or through the protoplasm adjacent to the reserve food in the cells of higher animals or plants. The products of digestion pass through the protoplasm, the protoplasm acting as a membrane. Having been absorbed, the simple substances produced in the digestive process are recombined and built up into living protoplasm, through the agency of enzymes. This synthesis of foods into protoplasm is assimilation. Very little is known as yet about this important process.

Respiration.—Almost without exception living things require oxygen. Many animals and plants get oxygen from the air and others from the oxygen which is dissolved in water. There are, however, some kinds of plants and animals that normally live in situations almost or wholly devoid of uncombined oxygen. Some of these organisms would die if transferred to situations which had even a small amount of free oxygen. Such organisms require some oxygen in their metabolism, but they secure it from combinations in which it occurs.

The oxygen which is taken into the body is consumed in various ways, some of it in the oxidation of protoplasm and its constituents, and some in the elaboration of various cell products. The combination of oxygen with protoplasm and its constituents and with foods of various sorts results finally in the formation of water and carbon dioxide. Other gases also arise as the result of metabolic activity. These gases must be eliminated and their elimination is an essential part of respiration.

In the simple animals and plants dissolved oxygen diffuses directly through the surface of the organism into the protoplasm. Thence by diffusion and protoplasmic currents it is carried to all parts of the cell where it is used in oxidative processes. In many small aquatic multicellular animals and plants with few layers of cells the dissolved oxygen may readily diffuse through the intervening cells to those which lie deeper. The distribution of dissolved oxygen to the various cells in higher plants and animals requires a transport system and is discussed in a later chapter.

Excretion.—Metabolism results in the formation of various gases, water, and other compounds, many of which are nitrogenous. Many of these substances are of no value in the body or would be harmful if allowed to accumulate. The process of their elimination is called *excretion*, and the waste materials *excretions*. While technically the gases resulting from metabolism might, since they are waste materials, properly be called excretions, their elimination is usually included under respiration. The waste substances pass through the cell membranes to the exterior, or in some of the protozoa they are gathered up by the contractile vacuoles and voided through the outlets of these organs. In higher animals excretions are collected by the blood and lymph, from which they are then separated by special organs.

Plants in the course of their metabolic activities produce a number of non-gaseous substances which are often of no further use to the plant cells. Such substances may be considered excretions. These are disposed of in various ways.

Secretion.—The cell is to be regarded as a laboratory or factory in which a multitude of chemical processes are taking place. Some of these processes have already been discussed. All cells produce certain chemical compounds which may be used in the chemical processes going on within the cell or in cavities adjoining the cells. Such products are *secretions* and the process of producing them is given the name *secretion*. Secretions differ from excretions in that they are used in performing some function for the body, while excretions cannot ordinarily be used by the organism. The actual processes involved in the production of excretions and secretions are very similar and the methods by which these substances are discharged from the cells of multicellular animals may be identical. Many of the secretions which are discharged from the cells are first stored in the cells as granules which finally break out of the cell at the exposed end and then become liquid or gaseous. Other secretions produced as liquids within the cell diffuse out and escape as rapidly as formed, are absorbed by other cells, or are carried in the blood stream. Such secretions may perform their functions at a considerable distance from the cells where they are elaborated. Secretions are very diverse in their functions. Some aid in digestion, others give protection because of their odor or because of poisonous qualities, some serve as lubricating material, others oxidize readily with the production of light, and there are still other kinds performing other functions. The diversity of functions served by secretions is indeed very great.

Single-celled animals and plants produce all the secretions required for carrying on chemical processes within their single cells. In higher animals and plants specialized cells may be set aside chiefly for the production of certain secretions. Localized groups of these cells are called glands. The structure of glands is considered in Chap. VI.

Growth.—Growth is characteristic of living organisms. It is due to the conversion of foods into protoplasm at a more rapid rate than protoplasm is being broken down in catabolic processes. Cells are strictly determinate in size, the size of any particular kind of cell in any organism being fairly uniform. When the cell has reached the limit of its size it may divide. The half-sized cells then grow to normal size. Thus the growth of the cell is due to the increase in the quantity of protoplasm. Increase in size of many-celled organisms is usually due to multiplication of cells and to the growth of the half-sized cells to normal. Increase in the size of the cell may not be wholly due to increase in the quantity of protoplasm. Fat cells increase in size because of the deposition of globules of fat, a process which may be continued until there is much more fat than protoplasm. In plant cells and certain animal cells volume may be increased by the imbibition of water which may be stored in vacuoles. In such extreme cases as those mentioned the quantity of protoplasm may be actually decreased although the cell may be larger. In every case where growth occurs it is due to the activity of the protoplasm. This is true in multicellular as well as unicellular organisms.

Reproduction.—Reproduction is likewise characteristic of living beings. In unicellular organisms, and only in these, reproduction is equivalent to cell division, for obviously a cell cannot reproduce its kind without a cell division of some sort. In higher organisms reproduction usually involves the formation of special cells, the germ cells, which by their division, with rearrangement of the resulting cells, give rise to new organisms. Here reproduction involves cell division too. An account of cell division is given in Chap. IV and a detailed account of reproduction in Chap. IX.

Protoplasmic Movement.—One of the attributes usually ascribed to living organisms, distinguishing them from non-living matter, is the power of independent motion. This power resides in the protoplasm. Most animals at some stage in their existence, many plants of the lower orders and the swarm spores of other low plants are motile. Higher plants are not capable of locomotion, but within their cells the protoplasm may undergo movement such as *streaming* or *flowing*. Naked plant cells and some forms of unicellular animals frequently progress by a type of protoplasmic movement which is so characteristic of the protozoön Amœba that it has come to be called *amœboid* movement. Other types of movement are *ciliary* and *muscular contraction*, the latter of which is described in a later chapter.

Flowing and Amœboid Movement.—In many cells the protoplasm frequently travels as if in channels, particle following particle, carrying plastids, food vacuoles, and cell inclusions along with it. When the course of such a stream is a closed circuit, the movement is known as *cyclosis*. When an amœba moves it thrusts out one or more lobe-

like processes, called *pseudopodia*. Then the body is pulled forward or flows forward. *Amœba verrucosa*, an amœba with a very viscous outer layer or ectosarc, puts out normally a single pseudopodium in contact

FIG. 25.—Diagram illustrating the movements of a particle of soot attached to the outer surface of *Amœba verrucosa*, in side view. *X* marks the location of the soot particle in position 4 of the amœba. In position 5 the particle is still at *X* but the figure has been raised a trifle in order to show the outline of the amœba. (*From Jennings.*)

with the substratum. The protoplasm of the upper surface flows toward the tip of the pseudopodium, while the protoplasm of the lower portion flows to the rear, thence to the upper surface and to the anterior end. Thus this amœba acts like an elastic sac filled with a viscous mass which creeps forward within the sac. By mixing soot in water containing Amœba so that particles of the soot adhere to the surface of the animals, one may demonstrate this movement, which is illustrated in Fig. 25. In *Amœba proteus* a number of pseudopodia may be thrust out. The anterior end is elevated, thrust out, and then brought in contact with the substratum to which it adheres. The posterior portion of the body is now brought forward by contraction of the protoplasm and this material forms a new anterior end. This may be demonstrated by mounting the animals on the edge of a slide, in a

FIG. 26.—Apparatus for the study of locomotion in Amœba in side view. It consists of a glass slide with a polished edge and two projecting cover glasses which form a groove in which the specimens are kept. It is used on a horizontal microscope. (*From Dellinger in Journal of Experimental Zoölogy.*)

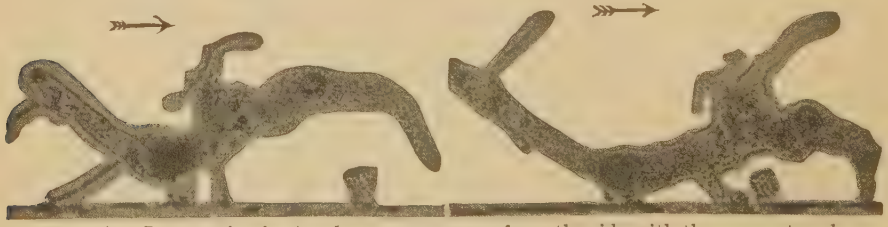

FIG. 27.—Locomotion in *Amœba proteus* as seen from the side with the apparatus shown in Fig. 26. *A* and *B* show the extension and attachment of a slender pseudopodium. Other pseudopodia are moving forward. (*From photomicrographs by Dellinger in Journal of Experimental Zoölogy.*)

groove formed by the projecting edges of two cover glasses as in Fig. 26, and examining them with a microscope in a horizontal position. Their movement then appears to be a sort of walking, as shown in Fig. 27.

There is much to indicate that the surface of an advancing pseudopodium has a lower surface tension than exists elsewhere, as has been stated in an earlier section. Pressure of the surface film at other places would force out a pseudopodium at the weakened portion. How the change of surface tension is brought about is not well known, but may be due to either external or internal agencies.

Amœboid movement occurs in the protozoa provided with pseudopodia, in some naked plant cells, and in some cells of higher animals, namely, white blood corpuscles and pigment cells. Some other cells, as the germ cells, which originate in one location and migrate to another at some distance probably use this form of locomotion during their migrations.

FIG. 28.—Fibrillar structure of cilium of Stylonychia. (*From Dellinger in Journal of Morphology.*)

Ciliary and Flagellar Movement.— Many small animals, such as Paramecium, wheel animalcules (rotifers) free-living flatworms, nemertean worms, and the aquatic larvæ of many animals are provided with numerous *cilia*, covering a portion or all of the surface of the body (Fig. 18). The cilia are minute hair-like projections capable of rapid vibration.

Each cilium has an elastic outer layer containing one or more contractile protoplasmic elements within it. The structure of a cilium of Stylonychia

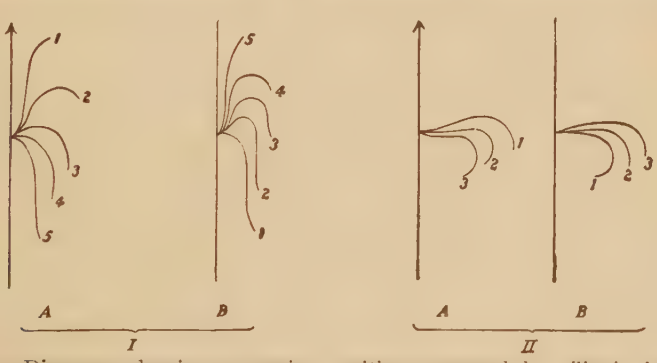

FIG. 29.—Diagrams showing successive positions assumed by cilia in locomotion. *A*, positions assumed from the beginning of the beat at 1; *B*, positions assumed during the return stroke beginning at 1. (*From Verworn.*)

is shown in Fig. 28. Each large cilium of this and similar forms is regarded as being formed of several cilia of ordinary size fused together. Contraction of the protoplasmic elements on one side bends the cilium in that direction. The elasticity of the sheath returns the cilium to the original position as soon as the contractile elements relax. The active stroke is rapid and involves the movement of the whole cilium while the return stroke is slow and begins at the base and like a wave runs along the cilium to its tip (see Fig. 29). The cilium thus presents the maximum friction in one stroke and the minimum in the reverse. Neigh-

boring cilia usually beat in unison or in waves, which is believed to be due to certain fibers connecting their bases with each other within the cell, as in Fig. 30.

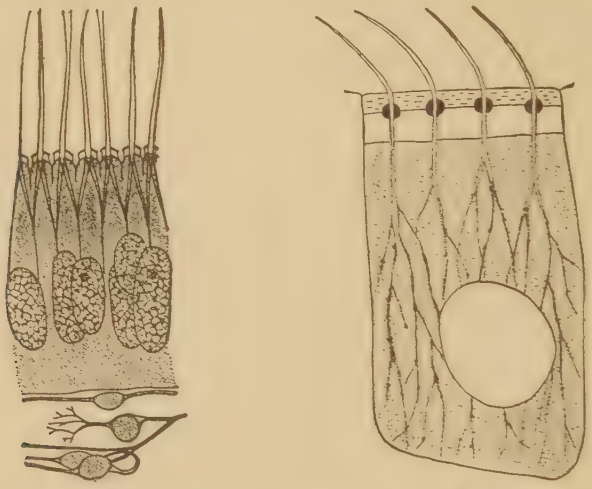

FIG. 30.—Ciliated cells, showing connections between the cilia within the cells. *A*, from the gill of a mollusk; *B*, from an epithelial cell. (*A after Grave and Schmitt. B after Saguchi; from Sharp, Introduction to Cytology. McGraw-Hill Book Company, Inc.*)

Many higher animals have inner surfaces covered with ciliated cells. Thus in the frog, currents produced by cilia continually carry small particles and the mucous secretion of the mouth down the esophagus to the stomach. In the mammals and probably in most other air-breathing vertebrates solid particles inhaled with the air are caught on the ciliated surfaces of the trachea and bronchi and are swept up into the throat by the action of cilia.

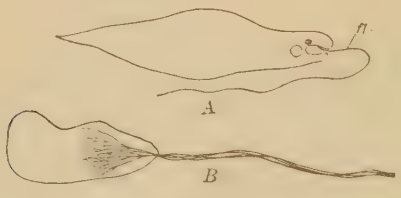

FIG. 31.

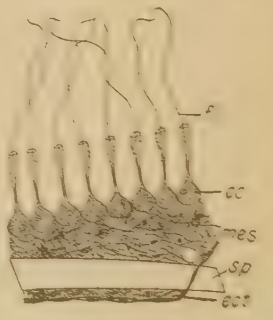

FIG. 32.

FIG. 31.—Euglena. *A*, outline showing flagellum (*fl*). *B*, the fibrils of the flagellum. (*A, original; B after Dellinger in Journal of Morphology.*)

FIG. 32.—Portion of cross-section of the sponge Grantia. *cc*, collared cells of endoderm; *ect*, ectoderm; *fl*, flagellum of collared cell; *mes*, mesoglœa; *sp*, spicule (portion only). (*Original.*)

Flagella differ from cilia chiefly in their greater length. When present they are few in number, there being from one to eight (rarely

more) to the cell. Flagella may beat regularly in one plane, as do cilia, or they may have a rotary motion which may involve the whole flagellum or only the free end of it, or the movement may be irregular, involving any portion of the flagellum. It has been shown for Euglena (Fig. 31) that the flagellum is composed of an elastic peripheral layer within which are several contractile threads extending throughout the length of the flagellum. The movement is due to the contraction of these threads. The movement of an organism propelled by flagella is jerky or erratic. There is rarely the gliding movement which is characteristic of animals which employ cilia in locomotion. Flagella are the normal organs of locomotion in one group of the protozoa, and in some plant cells, and occur rarely as cell organs in higher forms. They occur singly on the endoderm cells of the cœlenterates, and in sponges each cell of the radiating tubes (Fig. 32) is provided with a flagellum and a protoplasmic collar surrounding the base of the flagellum. In these two groups of animals the flagella serve to create currents of water which circulate through the cavities of the animals.

Responses to Stimuli.—A characteristic property of living matter is its tendency to change in various ways as a consequence of alterations in other things near it. This is not a diagnostic quality, however, since many non-living things change in response to modification of surrounding conditions. While the response of living things is sometimes enormous, relative to the stimulus which causes it, not even this is a property of living matter alone, since a slight movement of a lever may set a whole train of freight cars in motion. Responses to stimuli by protoplasm are, however, highly complex, and in this complexity lies the most significant difference between them and responses of non-living matter.

A stimulus is any change of sufficient magnitude to cause a change in protoplasm within the region of modification. It may be a change external to a living thing, as in light, temperature, chemical substances, sound, pressure, or electric current. Or the stimulus may come from within the organism, as by osmosis, electric charges, chemical substances, pressure, or nerve impulses. Not every change is a stimulus, since the modification must have a certain degree of suddenness to produce a response. A very gradual change in the intensity of light may have no observable effect, while a sudden change of the same amount produces a marked reaction.

Responses are of very different sorts. Muscle cells and many others contract. Gland cells produce secretions. Pigment cells in the skin of a frog, which are highly branched and diffuse when at rest, contract into a small compact mass in response to light, thereby changing the animal's color. Streaming of protoplasm in plant cells stops in response to an electric current. A chemical substance in the retina of the eye of vertebrate animals is decomposed by light. The electric organs of certain

fishes develop a high potential difference, and produce a series of discharges. The light of a firefly or other luminescent organism is due to oxidation of a specific substance, the chemical energy being directly transformed into the energy of light. Often a cell gives no visible response, but initiates a current of some kind which stimulates more distant cells.

The nature of the response is determined by the nature of the responding protoplasm, not by the kind of stimulus. A muscle cell contracts, no matter whether the stimulus is chemical or electrical. A gland cell secretes, and its product is always the same, regardless of what started its activity. Paramecium, if stimulated mechanically or chemically, backs away, turns through an angle away from its oral side, and starts forward again (the *avoiding reaction*).

The extent of a response is, in general, rather definitely fixed for any given cell. If the cell responds at all, it does so to its full capacity. An organ made of many cells may respond in various degrees, depending on whether few or many of its component cells join in the response. How many cells respond depends on the intensity of the stimulus. Each individual cell, however, follows the "all-or-none" rule of acting either at its maximum capacity or not at all.

Responses of different parts of an organism are coordinated either by chemical substances or by conduction of impulses. Chemical substances produced in response to a stimulus at one place may diffuse, or be carried, to another place and stimulate activity there. Substances that exercise such a control are known as *hormones* or *endocrine secretions*. The other means of control, by conduction, is an inherent property of all protoplasm. Amœba, for example, may be stimulated at one point, and respond by producing a pseudopodium elsewhere. Something is conducted through the general protoplasm to produce this result. In Hydra, the outer ends of ectoderm cells may be touched, whereupon the fibers at their inner ends contract. In higher animals there are complex systems of nerve cells whose function is that of conducting such impulses, thereby effecting a control of most of the physiological processes.

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CHAPTER IV

CELL DIVISION

Following the discovery of the universality of cells in living things, one of the most pressing biological questions had to do with the origin of cells. The founders of the cell theory believed that cells might arise either by a process of division of a preëxisting cell, or by "free cell formation." In the latter, cells were thought to crystallize out, as it were, from a formative or nutritive substance, the "cytoblastema." This method was considered to be the usual one. By 1855, however, biologists had arrived at the conclusion that cells arose only from preëxisting cells and this doctrine was summed up in that year by Virchow, the famous pathologist, in the words, "*omnis cellula e cellula.*"

Discovery of Cell Division.—While the origin of cells from cells was thus early established, the mechanism by which cells originated from other cells was not known until in the seventies and eighties of the last century. This apparent slowness was probably due to the fact that investigators were concerned in verifying the cell theory. It was also due in part to the want of good lenses, in part to the fact that staining methods were in their infancy, and that no accurate method of section cutting had been devised. These early investigators of cell phenomena had frequently to improve methods or devise entirely new ones and to design new apparatus for their work. They labored under great difficulties. It is not surprising, therefore, that early ideas of cell division were erroneous. Thus, Remak, in 1855 and 1858, described what he considered typical cell division as follows. The nucleolus, according to his account, divides first, followed by the division of the nucleus by simple constriction in the middle so that each half of the nucleus contains half of the nucleolus. Then, he thought, the cell body divides by progressive constriction about the middle of the cell. This scheme was accepted for some years as being the usual, perhaps universal, mode of cell division; but in the early seventies of the last century it became evident that such simple cell division is by no means so common as was at first supposed. Schneider, in 1873, observed a much more complicated process, which involved the resolution of the chromatin of the nucleus into bands and separate bodies, and the formation of a spindle-like object composed of fine threads. This process was soon thereafter witnessed by other biologists in a variety of plants and animals, and is now regarded as nearly universal. To it the names *mitosis* and *karyokinesis* are applied.

The latter term is the more descriptive, but the former is more often used.

General Course of Mitosis.—The general course of events in mitosis is illustrated in Fig. 33, which represents cleavage in the eggs of the marine snail Crepidula. These eggs are heavily laden with yolk, most of which is omitted from the figures, which accounts for the irregular form of some of the illustrations.

In one of these eggs which is not in any stage of division, the chromatin of the nucleus is in a very diffuse state, and may appear as particles of various sizes, mostly very fine, or in minute threads tangled in a complex manner. As division commences, this chromatin is collected or condensed into larger particles, at first in the form of coarser threads, later into short rod-like bodies, the *chromosomes* (Fig. 33, *C*). During this condensation of the chromatin, there appears in the cytoplasm just outside the nucleus a pair of small bodies, the *centrosomes* (containing *centrioles*), with fine lines connecting them in a spindle-shaped group, and other fine lines, the *astral rays*, radiating from each centriole (*B*). The spindle of fine lines enlarges until the centrosomes are on nearly opposite sides of the nucleus (*C*). The nuclear membrane is then dissolved, and the chromosomes are located in the middle region of the spindle (*D*). Here each chromosome divides into two parts (*E*), and one half of each chromosome moves, or is drawn, to one end of the spindle, the other half to the other end of the spindle (*F*, *G*). Two groups of chromosomes are thus formed, each containing a half of every chromosome present before the division.

At the ends of the spindle, the chromosomes of each group are reconstructed into a new nucleus (*H*, *I*). During the early part of this reconstruction, or even before it begins, the cytoplasm of the cell is constricted between the two groups of chromosomes, and finally a cell membrane is passed completely across what had been the middle or equatorial plane of the spindle (*I*). Two new cells are thus formed, each essentially like the one from which they were produced, though smaller.

The general course of mitosis, as just described, is followed by most cells in division. There are differences in the details, however, some of which merit further attention.

Condensation of the Chromosomes.—The arrangement of the chromatin in a resting nucleus is subject to variations which, so far as can be ascertained from its appearance, are mostly minor. Whether the chromatin appears as fine granules or as minute threads is unimportant. It would be important to know whether, in this diffuse material, the future chromosomes are already separate entities. In some organisms, the chromosomes appear to be distinct and separate at all times. In certain plant cells, the chromatin of the resting cell is in the form of irregular clumps with ragged edges, which are of the same number as are the chromosomes later, and which are in fact the chromosomes. In the

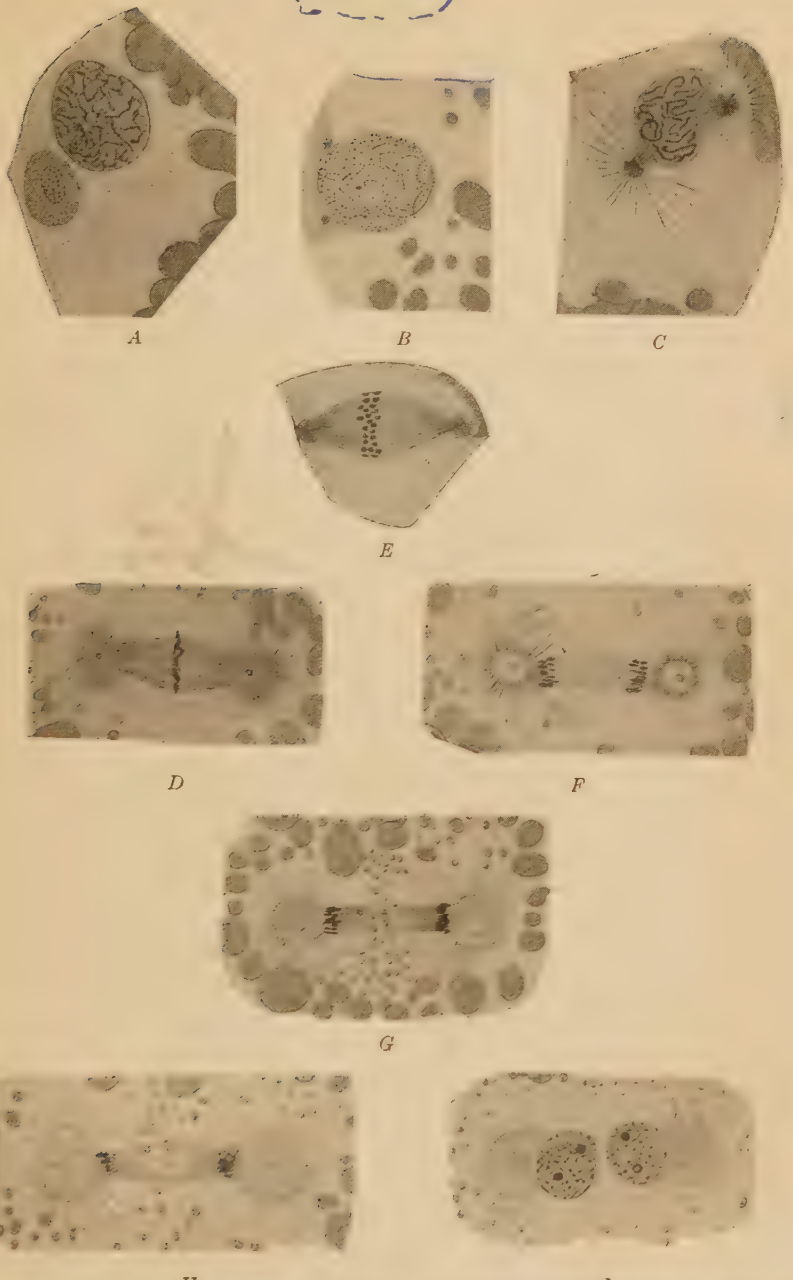


FIG. 33.—Division of the egg of Crepidula, only parts of cells shown. *A*, cell not in division, with centrosphere below nucleus at left; *B*, two asters and spindle formed from centrosphere, at left of nucleus; *C*, chromosomes formed in nucleus, spindle well developed; *D*, chromosomes on equator of spindle; *E*, chromosomes divided in two; *F*, halves of chromosomes moving toward ends of spindle; *G*, chromosomes at ends of spindle, adjoining asters; *H*, chromosomes being reconstructed into a nucleus at each end of spindle; *I*, reconstruction of nuclei practically complete, cell body divided in two between nuclei. (*After Conklin.*)

giant salamander, the resting nucleus is composed of a number of vesicles, each of which is probably one of the chromosomes (Fig. 34). The chromatin in these vesicles is so diffuse that, were the vesicles less rounded and more tightly compressed against one another, it would be easy to

FIG. 34.—Resting nucleus of the giant salamander, showing the chromosomes distinct and separate as vesicles, in which, however, the chromatin is very diffuse: early and late stages. (*From B. G. Smith in Journal of Morphology and Physiology.*)

overlook the separateness of the chromosomes. Chromosomal vesicles are known in a number of other animals, and the existence of separate and distinct chromosomes even in the resting nucleus is probably fairly common.

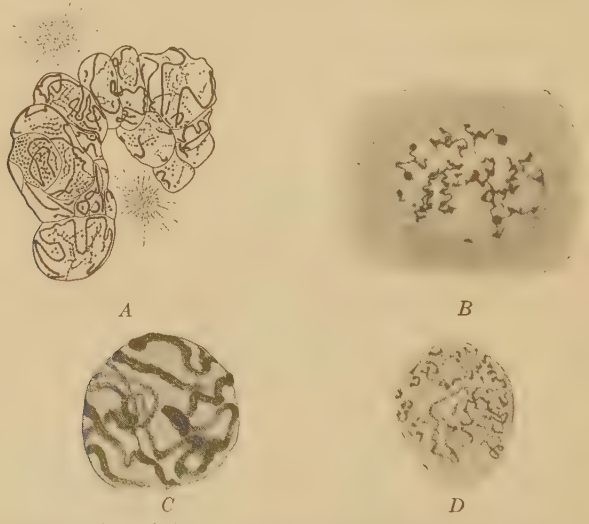


FIG. 35.—Condensation of the chromatin in early stages of mitosis. *A*, egg of giant salamander; *B*, sea urchin; *C*, root cells of Clivia; *D*, spermatogonia of spotted salamander. (*A from B. G. Smith in Journal of Morphology and Physiology; B from Danchakoff; C from Van Camp; D from Janssens.*)

In the giant salamander, when the chromatin condenses into distinct bodies, it collects into a conspicuous thread, each chromosome separately (Fig. 35, *A*). The distinctness of the chromosomes is not, however, always so plain in other animals. In the egg of the sea urchin,

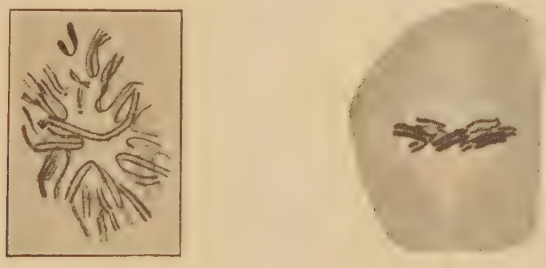
threads are formed (Fig. 35, *B*), but whether these are separate, or connected by fine, partly invisible threads is debatable. The root cells of certain plants have heavy threads (*C*), which have still more the appearance of being connected into a continuous band, while the continuity of the corresponding threads in the salamander (*D*) has been repeatedly described. Even in these latter cells, however, the chromosomes may

A *B* *C*

Fig. 36.—Chromosomes of various shapes, shown just before they are arranged across the middle of the spindle. *A*, oögonium of the beetle Dytiscus (*from Debaisieux in La Cellule*); *B*, spermatogonium of arrow worm Sagitta (*from Bordas in La Cellule*); *C*, egg of giant salamander (*from B. G. Smith in Journal of Morphology and Physiology*).

really be distinct; minute breaks in the strand might easily escape observation, so that it is difficult to determine whether the chromosomes are discrete or continuous with one another. The facts of heredity in certain animals indicate that the chromosomes maintain their individuality, no matter what their apparent condition may be in the several stages of the cell's existence.

Variations in Chromosomes and Their Behavior.—The chromosomes may vary in shape from small, nearly spherical bodies, to long slender rods



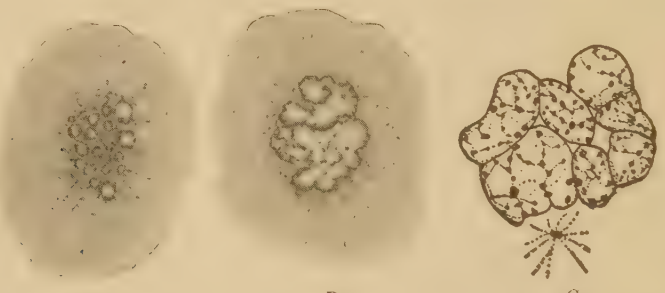
A *B*

Fig. 37.—Splitting of the chromosomes. *A*, peritoneum of the salamander Amblystoma; *B*, spermatogonium of the stonefly Perla. (*A from Parmenter, B from Nakahara, in Journal of Morphology.*)

or threads (Fig. 36). Often the chromosomes of the same cell differ greatly in size and shape. When the chromosomes are long, they may be either straight, or a hook, or a V, depending on whether, in their movement towards the end of the spindle, the motion of the chromosomes starts at one end or at some middle point.

The division of the chromosome takes place lengthwise when the chromosomes are long rods (Fig. 37, *A*). In short and rounded chromo-

somes it is difficult to relate the plane of division to their shape, but there probably is a definite relation of this sort. In some cells the division appears to occur only after the chromosomes are arranged on the equator of the spindle (Fig. 37, *B*), but in others it takes place much earlier.



A *B* *C*

FIG. 38.—Reconstruction of nuclei through imbibition of liquid by the chromosomes, to form vesicles. *A* and *B*, early and late stages of vesiculation in the egg of the sea urchin, in which the vesicles fuse (*from Danchakoff in Journal of Morphology*); *C*, embryo of Fundulus, vesicles not fusing (*after Richards, from Sharp's Introduction to Cytology. McGraw-Hill Book Company, Inc.*)

The number of chromosomes differs in different animals. In the nematode worm *Ascaris megalocephala* it is four; in the fruit fly, *Drosophila melanogaster*, there are eight chromosomes in each somatic cell; in one of the bugs there are 22; and in man 48 chromosomes. In some animals the number in the two sexes is not the same, being larger in the female in most such species.

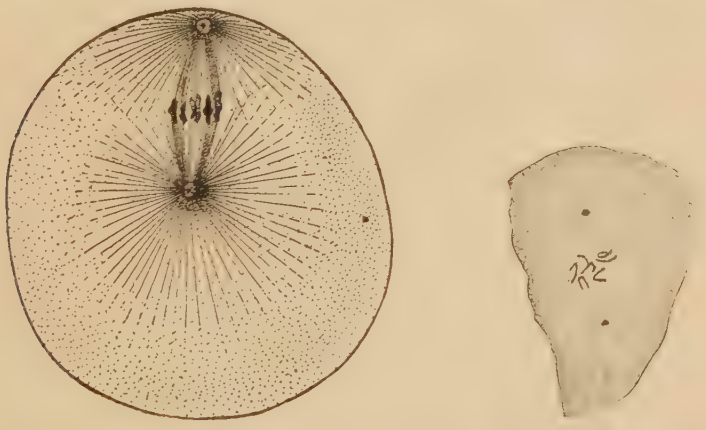
A *B*

FIG. 39.—Vesiculation of chromosomes by formation of cytoplasmic film around each chromosome; *A* early, *B* late stage. The vesicles do not fuse. (*From B. G. Smith in Journal of Morphology and Physiology.*)

Reconstruction of the Nuclei.—The transformation of the chromosomes into a new nucleus, after they have reached the end of the spindle, is often an obscure process. In many cases it is accomplished by the conversion of the chromosomes into vesicles. This is clearly the case in the segmenting eggs of sea urchins (Fig. 38, *A* and *B*). The chromosomes appear to imbibe the surrounding liquid and swell until they meet and apparently fuse. In the fish, Fundulus (*C*), the vesicles are formed by imbibition, but do not fuse. In the giant salamander vesicles are formed (Fig. 39, *A* and *B*), not by imbibition of liquid, but by the formation of a film out of cytoplasmic material around each chromosome. The chromatin becomes very diffuse within this film. In this salamander the vesicles do not fuse but remain distinct throughout the resting stage (Fig. 34). Formation of new nuclei by vesiculation of the chromosomes

provides means by which chromosomes may preserve their identity through successive cell divisions. As stated above, the facts of heredity, together with certain cytological observations, indicate that the chromosomes do thus maintain their individuality. It is not improbable, therefore, that vesicle formation occurs in many cases where it is not obvious, and that it may be a common way of reconstituting nuclei. Another method is by the union of the chromosomes, end to end, in a long thread, from which the chromatin diffuses out in fine branches or a network. This method was described early in the study of cell division, and was long regarded as the usual way of converting distinct chromosomes into the diffuse state of resting cells.

The Spindle.—The spindle, composed of fibers, astral rays, and centrosomes, is a very conspicuous object in the eggs of Crepidula (Fig. 33).



A *B*

FIG. 40.—Dividing cells possessing prominent spindles. *A*, egg of the mollusk Diaulula; *B*, egg of Thysanozoön. (*A from Wilson, The Cell, after MacFarland; B from Schockaert in La Cellule.*)

They are similarly prominent in many other animals (Fig. 40). In the higher plants centrosomes are wanting, though the spindle fibers are usually well developed (Fig. 41). Some animal cells are practically devoid of a visible spindle, at least in cells prepared by the usual methods, yet in these cases and in plant cells without centrosomes the chromosomes divide, and their halves move apart, indicating that the spindle is probably of secondary importance in the mechanism of cell division.

In most cells, the spindle is formed outside the nucleus while the nuclear membrane is still intact. Occasionally this membrane in such cells appears as if it were being pushed in by the spindle fibers (Fig. 42). In some species a spindle is first formed outside the nucleus, but this degenerates and is replaced by fibers formed within the nucleus; and in certain protozoa, insects, rotifers, and some others, the spindle

fibers develop from the first inside the nucleus (Fig. 43), though the centrosome may be produced outside.

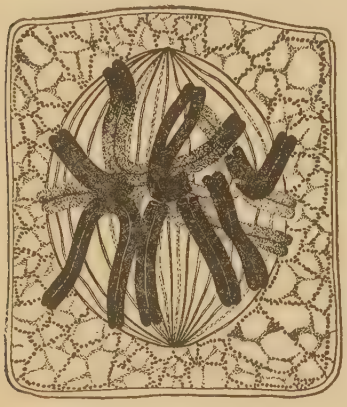


FIG. 41.—Mitosis without centrosomes in a cell of the root tip of the hyacinth. (*From Dahlgren and Kepner, Principles of Animal Histology.*)

FIG. 42.—Spindle formed outside the nucleus, with spindle fibers appearing to push in the nuclear membrane; segmenting egg of Unio. (*From Dahlgren and Kepner, Principles of Animal Histology.*)

Variations in Division of Cytoplasm.—Plant cells differ from animal cells in the method of dividing the cytoplasm into two parts at the time

FIG. 43.—Intranuclear spindle in the rhizopod protozoön Euglypha. (*From Wilson, The Cell, after Schewiakoff.*)

FIG. 44.—Formation of the cell plate in a dividing cell of the root tip of the hyacinth. The thickenings on the fibers of the spindle are the beginning of the process. (*From Dahlgren and Kepner's Principles of Animal Histology.*)

of mitosis. In most animal cells there occurs a constriction of the cell body in the equatorial region. This process of constriction continues until the cytoplasm is divided into two parts. In plant cells division of

the cytoplasm is accomplished by the growth of a cell plate at the median points of the spindle fibers. The position of the cell plate is first marked by thickenings on the spindle fibers (Fig. 44). These thickenings increase in size and number during the reconstruction of the nuclei and eventually a new cell wall is laid down in the plane which they occupied.

Amitosis.—Whether correctly or not, biologists have long distinguished two kinds of cell division, called *amitosis* and *mitosis*, respectively. Amitosis is essentially the type of cell division described by Remak, and involves no complicated visible mechanism. The word amitosis means, literally, not mitosis. The doubt concerning amitosis arises from the possibility that it is after all only a distorted form of mitosis, the distortion being due either to faulty preparation or to natural

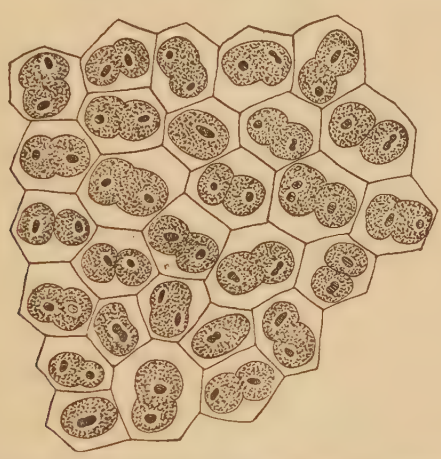


FIG. 45.—Amitotic division of the nuclei in the follicle cells of the cricket's ovary. Various stages of nuclear division are shown. (*From Conklin.*)

degenerative changes in the cells. Preparations of cells have in some cases been so defective that cell division was at first regarded as amitotic, but on closer examination revealed some of the features of mitosis. Also, in certain degenerate animals it appears that the process itself has become so modified that even the most perfect preparations of dividing cells resemble amitotic division very closely.

Further confusion has arisen from the fact that the nucleus of a cell may divide without any subsequent division of the cell body. This division is often called amitosis of the nucleus, but it is not amitotic cell division. Follicle cells in the cricket's ovary (Fig. 45) show nuclear division of this sort. The significance of such nuclear division is in doubt. In highly active cells, as pointed out in Chap. II, the nucleus may become branched or lobed. If the formation of two lobes should proceed to complete separation, two nuclei would result, and the separation might be

called amitosis of the nucleus. Such a division would hardly have any relation, however, to the phenomenon of cell division.

It is difficult to say, under these circumstances, how many of the supposed cases of amitosis are really such. Division that has the *appearance* of amitosis has been observed in old tissues; in degenerate parasitic animals; in certain one-celled animals where, as in Paramecium, there are two nuclei, one of which divides by amitosis, the other by mitosis, so that the division of the cell may be regarded as of either type; and in a variety of cases in which defective preparations may be responsible. Amitotic division of the nucleus alone has been described in embryos, in reproductive tissues, in regenerating structures, and some others. Probably these latter cases have no relation to cell division, though the term amitosis clings to them.

Even if most of the supposed cases of amitosis are really such, amitotic cell division is still of very limited occurrence in the animal kingdom. Also, it is of much less significance in biological theory than is the much more common method of mitosis.

Significance of Mitosis.—The significance of the mitotic method of cell division may be appreciated when one contemplates the fact that the process results in an approximately equal quantitative and qualitative division of the material of each chromosome. The equal *qualitative* division of the chromosomes is especially of great importance. It is the present-day conception, supported by a considerable body of evidence derived from breeding experiments and observation, that many of the substances (of whatever sort they may be) which determine the activities of the cell and also those which determine hereditary qualities (the *genes*, Chap. XII), are distributed along the length of the chromosomes. Much of this same evidence also indicates, as has already been pointed out, that the chromosomes retain their individuality even during the period when the chromatin is arranged in diffuse form, so that the chromosomes appearing in one cell division contain the same chromomeres as in the preceding division. This belief in the individuality of the chromosomes is supported by those cases in which the chromosomes become vesicular in form during reconstruction and remain as discrete vesicles during the resting period (Figs. 34, 39, *A* and *B*). According to this view certain chromosomes or groups of chromosomes are responsible for certain hereditary characters and probably for certain physiological activities depending on the elements contained in their chromomeres. If this assumption be correct, the longitudinal splitting of the chromosomes, with the resultant splitting of the longitudinally arranged chromomeres, is the only method by which the equal division of those substances which control cell activity and heredity may be assured.

Causes of Cell Division.—What starts the process of division in cells is not certainly known. Recent studies of the physiology of protoplasm

have demonstrated a close connection between cell division and the capacity of protoplasm for undergoing changes in viscosity. Colloidal substances in general can be changed from a semisolid to a semiliquid condition and *vice versa*, and protoplasm exhibits the same property. A rhythmical change in the viscosity of certain dividing eggs has been discovered, the protoplasm becoming more solid during the formation of the spindle, and more liquid in later stages. Furthermore, when these changes in viscosity are prevented by immersing the cells in solutions of certain substances, the process of cell division in the eggs is arrested. There is some reason to believe that increased viscosity in this case is due to withdrawal of water from the protoplasm, and that the change to the more liquid condition follows the imbibition of water. How the extraction and imbibition of water are brought about is uncertain, though changes in osmotic effects and in the permeability of the cell membrane may be responsible.

Other factors have often been proposed as inducing cell division. Some have suggested that changes in surface tension may initiate cell division, though this agent would be concerned chiefly or perhaps only with the division of the cell body, unless the surface tension of chromosomes and other structures in the cell be supposed also to change. Another suggestion is that the rate of oxidation is a factor in cell division, but it seems possible that changes in this rate are consequences, rather than causes, of cell division. Electrical phenomena have also been appealed to as causes of division, but too little is definitely known concerning the electrical charges in cells to apply this conception fully. It is sometimes explained that cell division tends to preserve a certain relation between the bulk of a cell and the area of its surface, but "tendencies" without a discoverable physiological foundation do not amount to explanations. There is still much uncertainty concerning the factors that initiate cell division.

Mechanism of Mitosis.—One of the older views in regard to the forces operating in mitosis was that the astral rays and certain fibers of the spindle were protoplasmic threads which were capable of contraction. According to this view these particular fibers, which are only half as long as the spindle, are attached to the chromosomes and the movements of the chromosomes is due to pulling by these fibers. Also the fibers of the asters have been supposed to bring about the constriction of the cell body and the consequent division of the cytoplasm. This conception of the function of the fibers is not without support at the present time. Originally evidenced only by observations on fixed and stained cells it has had within recent years some support from the experimental side. A long series of experiments in which dividing plant cells were subjected to solutions of various poisons has shown that these achromatic structures act as if the parts were made up of definite fibers which are thrown out of

their normal position by the action of the poison. Certain investigators have dissected out individual chromosomes from the dividing cells of salamander testes and occasionally have found a chromosome to which was attached a minute protoplasmic thread which they considered to be a portion of a spindle fiber. What causes these fibers (if they are fibers) to behave in the definite and orderly fashion which may be observed in mitosis is not known.

In connection with the above theory holding the fibers responsible for the mechanics of cell division, it was once thought that the whole process of mitosis was under the control of the centrosome which was supposed to be present in every cell. When it became known that the centrosomes behaved in a different manner in various cells and that, although they were non-existent in most plant cells, mitosis proceeded in an orderly fashion in such cells, the idea of the importance of the centrosome was abandoned. The splitting of the chromosomes is probably to be accounted for by some form of protoplasmic movement. It is not impossible, also, that their movement in mitosis is due, at least in part, to active migration of the chromosomes themselves.

The form of the mitotic figure, and particularly the spindle, has led to its comparison with the lines of force revealed by the arrangement of iron filings in the field of a horseshoe magnet. Such a comparison furnishes an excellent illustration or model, but it probably offers little to the solution of the mechanism of mitosis. Active migration of the protoplasmic substances, due no doubt to their chemical reactions, has been appealed to for an explanation of the movements of the chromosomes. Another view attributes these movements to the enlargement and collapse of multitudes of vesicles in the protoplasm. Further knowledge of the mechanism of mitosis probably awaits discoveries in the field of colloid chemistry.

Universality of Cell Division.—That cells originate only from pre-existing cells was affirmed in an earlier part of this chapter. Evidence secured from the observations of an enormous number of investigators working with both plants and animals substantiates that statement. No trustworthy evidence has been secured to show that cells originate in any other way than from cells or by any other method than cell division. Although it has been suggested that the nucleus may, in certain degenerate forms, arise from cytoplasm, there has never been satisfactory evidence for the idea. Indication of the continuity of certain specialized cell organs is also at hand. Plastids, such as chloroplasts, originate only from existing plastids by fission. Other cell organs besides chromosomes and plastids are known to divide and thus perpetuate themselves, but their maintenance and growth depend upon their relation to the cell. It is this division of the cell and its organs, and especially the equal qualitative division of the chromosomes, which furnishes the

mechanism by which the two cells resulting from the division of a parent cell resemble each other. It is through the operation of this mechanism that hereditary qualities are transmitted from parent to offspring.

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CHAPTER V

THE ORIGIN OF THE METAZOA

A comparison of a large series of animals shows great diversity of size, form, and complexity of structure. On the one hand are animals of striking simplicity, the entire animal being made of a single cell. Amœba, Euglena, and Paramecium are animals of this type. These and their allies comprise the group Protozoa. On the other hand are animals composed of many cells. In this group are Hydra, sponges, many kinds of worm-like animals, the starfishes, the clams, crayfishes, insects, and man. While very dissimilar in size and degree of complexity all these animals and their allies are much more complex than the protozoa. These complex animals are each composed of many cells and are called *metazoa.*

Formulation of the Problem.—Mere size does not distinguish metazoa from protozoa for the larger protozoa are of greater volume than the smaller metazoa. Nor does the distinction lie chiefly in the fact that metazoa are composed of many cells. The principal mark of a metazoan animal is the existence, among its many cells, of two fundamentally different kinds, namely, reproductive and non-reproductive, while in the protozoa the cell is always reproductive. Even in those species of protozoa whose cells adhere instead of separating after cell division there is but one kind of cell and that kind is capable of reproduction. The cells of a metazoan individual arise by the repeated divisions of a single cell, the fertilized ovum, and of its descendants, all of which adhere in a mass. Many of the cells thus produced surrender the function of producing new individuals. These non-reproductive cells in all but the simplest metazoa come to be of various sizes, forms and functions, and in all metazoa form a more or less massive structure known as the *body* or *soma.* In this soma those descendants of the fertilized ovum which do not give up the function of reproduction, and which are called reproductive or *germ* cells, are sheltered and nourished.

There can be little doubt that the metazoa originated from the protozoa, and the metazoan body from masses of protozoan cells. The nature of the species forming the evolutionary series that culminated in the simple metazoa cannot be directly ascertained because, being presumably soft-bodied, they disintegrated without having formed fossils. At any rate, no fossils have been found which could be interpreted as belonging to the series. Any attempt, therefore, to illustrate the pos-

sible steps in the evolution of the metazoa must proceed by inference from such existing species of protozoa, protozoan colonies, simple metazoa, and such common embryonic stages of the metazoa as seem to meet the requirements of the series. It is not at all probable that the species employed in illustrating the possible steps in the evolution of the metazoa were those actually involved.

Point of Departure.—The point of departure in any attempt to trace the origin of metazoa is obviously the single cell as it exists in the majority of protozoan species. In these species the cell carries on the functions of the body. It takes in food, digests it, and assimilates the products of digestion. Within this one cell are carried on the processes of respiration, secretion, excretion, and locomotion. It responds to stimuli, and it produces other cells. Thus the cell in such protozoan species carries on all its life processes independently of its fellows. Its reproductive processes, when these are asexual, as by fission, do not require the coöperation of another member of the species. It is only in sexual reproduction, which is the least common method in most protozoa, that the coöperation of another cell is required. This state of independence is exemplified in such protozoa as Paramecium, Euglena, Amœba, Chlamydomonas, and Vorticella. In a large number of species of this type the cells are motile. If they are sessile (attached) they may occur singly or in groups, but even in the latter case the cells have no organic union with each other. When cell division occurs in these species of protozoa the parts separate from each other. Even forms like Vorticella which are attached to the substratum by means of stalks release themselves from the old stalk which does not divide. The two cells swim about for a time, then settle down, and each secretes a new stalk. Those forms which are enclosed in gelatinous sheaths emerge from the old sheath after cell division.

Development of the Protozoan Colony.—In a much smaller number of protozoan species, however, the cells adhere at the conclusion of cell division. In some of these forms no more than two cells adhere, but in others the cells may remain attached after many cell divisions. As a result of this adherence colonies ranging from two to thousands of cells may be built up. The manner of adherence varies. In some species the original cell is surrounded by a jelly-like envelope within which the daughter cells remain, and these cells usually contribute to the formation of a larger mass of jelly. In certain stalked forms when the cell divides the daughter cells remain attached to the old stalk, but each daughter cell secretes stalk material. Thus each cell is attached by its stalk to the old stalk. The alternate division of the cells and the production of new stalks by the daughter cells give rise to a branching type of colony. If the cells adhere after cell division a more or less complex colony is built up whose morphological characters are dependent upon the

plane of division, the subsequent growth of the cells or of certain of their parts, and the development of new parts of cells. In accordance with these differences, different forms of colonies are produced.[1]

The forms of protozoan colonies are *linear*, *dendritic*, *gregaloid*, and *spheroid*. These types of colony are discussed and illustrated below.

Linear Colony.—The linear colony is the result of repeated cell divisions in one plane followed by incomplete separation of the resulting cells. *Ceratium candelabrum* (Fig. 46) illustrates the form of a linear colony. Such colonies are rare among the protozoa, but are common among the lower plants where they are best exemplified by the filamentous algæ of which Spirogyra is a common example.

Fig. 46.—A linear colony, *Ceratium candelabrum*. (*Modified from Lang, after Steinschütt.*)

Dendritic Colony.—Dendritic colonies have a branching form like trees. Good examples are Codosiga and Anthophysa. Codosiga (Fig. 47) is a stalked form. After a cell divides the two new cells remain attached to the old stalk but each cell begins to secrete a new stalk. With successive divisions followed each time by stalk formation a tree-like colony is produced. Anthophysa (Fig. 48) is composed of groups of flagellated cells borne on the tips of a branched stalk.

A series of dendritic colonies beautifully graded in complexity is exhibited by species of Vorticella, Epistylis, Carchesium, and Zoöthamnium. Individuals belonging to species of Vorticella are unicellular and never form organic colonies. Each individual is provided with a contractile stalk. Cell divison is followed by the complete separation of one or both cells from the old stalk. The free cells swim about and finally each attaches itself to some object by its aboral end and then produces a new stalk. The species of the other genera named above occur as more or less complex tree-like colonies. In some species of Epistylis there may be as few as two cells on a non-contractile stalk, but in *E. flavicans* there may be hundreds of individuals and many primary stalks with

[1] *Aggregations* or *associations* are sometimes formed by the more or less complete fusion of previously separate cells of the same species. Sometimes two or more cells simply adhere owing to the stickiness of portions of their surface; in other instances cell boundaries are broken down to such an extent that it is no longer possible to determine the limits of the individual cells. In all these aggregations or associations the nuclei retain their identity regardless of the degree of fusion of the cytoplasm. In structural form aggregations may resemble colonies from which they can be distinguished only by their method of origin. Colonies are formed by the division of single cells, while aggregations arise from the association of two or more cells which were at one time independent. Cell aggregations are omitted from further discussion in this chapter since it seems scarcely probable that they played a part in the development of the metazoa.

their branches imbedded in a mass of jelly of the size of a walnut or even of a base ball. Such a colony is a combination of the dendritic and spheroid types. Carchesium and Zoöthamnium differ from Epistylis in that certain of the stalks are provided with contractile elements.

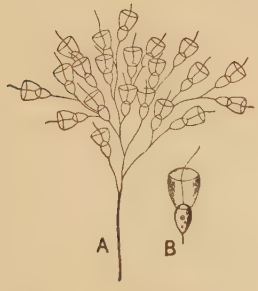

FIG. 47.—*Codosiga cymosa* Kent. *A*, tree-like form of colony; *B*, individual cell in detail. (*After Kent.*)

FIG. 48.—*Anthophysa vegetans* Müller. Spheroidal colonies arranged on a branching stalk, thus combining two types of colonies. The stalk is made up of many fibers. (*After Kent.*)

Gregaloid Colony.—Gregaloid colonies are of spherical, ellipsoidal, or indefinite shape, and they usually have a basis of gelatinous material throughout which the cells are strewn without regularity. *Microgromia socialis* (Fig. 49) and *Proterospongia hæckeli* (Fig. 50) illustrate this type of colony. Gregaloid colonies may be of no importance in the origin of the metazoa but attention has more than once been called to the marked similarity of certain features of Proterospongia to the sponges, a low group of metazoa.

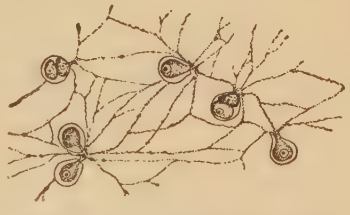

FIG. 49.—A gregaloid colony, *Microgromia socialis*. (*From Calkins's The Protozoa, The Macmillan Co.*)

Spheroid Colony.—Spheroid colonies are somewhat spherical or ellipsoidal in form. Their cells usually form a superficial layer in a gelatinous mass (Fig. 53). Stalks may connect the cells with a common center, as in Synura or in some species of Uroglena, while in other genera there may be no stalks.

Pandorina and Eudorina, lower members of the Volvocales, are excellent illustrations of spheroid colonies. The Volvocales took their origin, it may be supposed, from a form like Chlamydomonas, whose single cell is furnished with a nucleus, chloroplast, pyrenoid, stigma, vacuoles, two flagella, and a cell wall (Fig. 51). During the process of asexual reproduction it divides to form 2, 4 or 8 cells which are retained for a time within the cell wall. Finally the cell wall is changed to mucilage and the daughter cells are released to lead independent existences.

It is obvious that if these cells remained within the cell wall until the occurrence of the next cycle of asexual reproduction a simple colony would be formed.

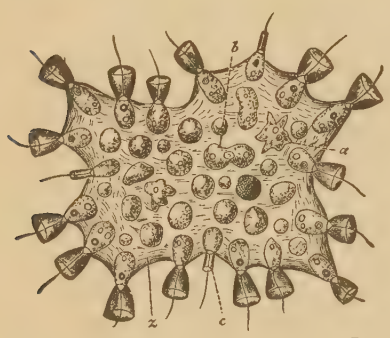

FIG. 50.—A gregaloid colony, *Proterospongia hæckeli*. (*From Hegner's College Zoölogy, The Macmillan Co.*)

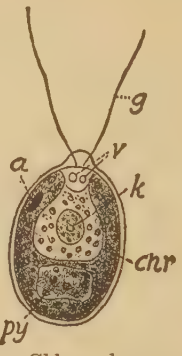

FIG. 51.—Chlamydomonas, a single vegetative cell. *a*, stigma; *chr*, chromatophore; *g*, flagellum; *k*, nucleus; *py*, pyrenoid; *v*, vacuoles. (*From Hegner after Oltmanns.*)

Pandorina (Fig. 52) is a colony consisting of a compact group of 8 to 32 cells, the usual number being 16, arranged in the form of a small sphere. The whole is embedded in a secreted jelly-mass to which each cell contributes. Since the cells are in contact their sides are flattened. Each cell resembles a little pyramid whose apex is at or near the center of the sphere. A slight step in advance of Pandorina is presented by *Eudorina elegans*. Eudorina (Fig. 53) is a colony of 32 cells situated rather far apart and near the surface of a nearly spherical mass of jelly. In Pandorina and Eudorina all cells of a colony are similar to one another.

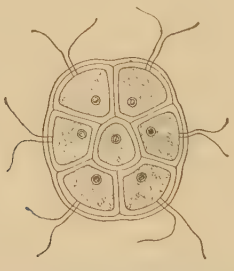

FIG. 52.—*Pandorina morum*, a spheroidal colony.

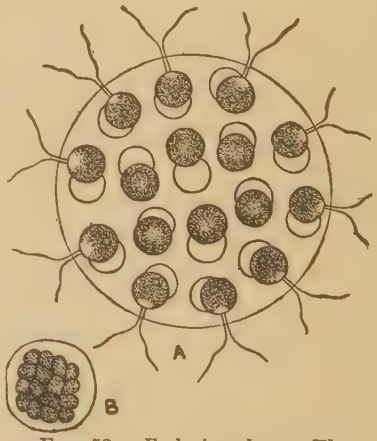

FIG. 53.—*Eudorina elegans* Ehrenberg, a spheroid colony. *A*, adult colony, ×475; *B*, daughter colony produced by the division of one of the cells of *A*, ×730. (*From West after Goebel.*)

Origin of the Soma.—The beginnings of the soma may be seen in the genera Pleodorina and Volvox which are higher members of the series of Volvocales. Pleodorina and Volvox present a considerable advance in complexity over Pandorina and Eudorina in that certain of their cells have become incapable of reproduction. These sterile cells constitute the soma or body. As will be seen in the description of *Pleodorina illinoisensis*, the soma in its earliest appearance is insignificant in size but in *Pleodorina californica*, and in the species of Volvox, the soma is of greater volume. In still more complex animals than these, it encloses, protects, and nourishes the reproductive cells. In such animals the soma, because of its size and the degree to which its cells have become modified in form and function, and because of its seeming permanence and the apparently temporary character of the germ cells, is frequently looked upon as the most important part of the organism. As a consequence it is the soma which is chiefly discussed in treatises on morphology, taxonomy, physiology, and evolution of metazoan animals.

Pleodorina illinoisensis resembles *Eudorina elegans* in form and appearance. It may, indeed, be only a variety of *Eudorina elegans*. It is ellipsoidal and has 32 cells embedded in a jelly matrix. In the typical condition, however, four cells at the anterior pole are smaller than their fellows. These four cells are sterile. *Pleodorina californica* is much larger than *P. illinoisensis* and its cells are more numerous. Its cells are always of two sizes, large and small, the proportion of small sterile cells to the total number being much higher than in *P. illinoisensis*.

In the genus Volvox, the species show considerable range in size and complexity. The number of cells in the mass ranges from 200 to 2,000 in the smallest species, *Volvox aureus;* while *V. rousseletii* has more than 50,000. In all the species the cells are arranged near the surface of a hollow sphere of a gelatinous or mucous material. In old specimens of *V. perglobator* the cells are widely scattered while in *V. rousseletii* they are compactly arranged. The cells of Volvox are of two sizes, the small somatic cells being in great abundance.

New colonies of the species of Pandorina and Eudorina may be formed by the repeated division of each of the old cells of the parent colony. In this manner as many new colonies are formed as there were cells in the parent. In Pleodorina only the large cells are capable of reproduction in this manner, the somatic cells having lost this power. In Volvox the function of reproducing asexually is possessed only by a small number of large cells, the *parthenogonidia*. The parthenogonidia are irregularly distributed among the somatic cells from which in their earlier stages they cannot be distinguished. Each parthenogonidium is provided with chloroplasts and in young stages with two flagella. Numerous protoplasmic strands connect the parthenogonidia with the neighboring somatic cells, in the same manner as the somatic cells are connected with

one another. Sexual reproduction occurs in all the genera of the Volvox series by means of specialized cells, the mature germ cells, two of which fuse to form the oösperm. The oösperm then divides to form a new individual. The variations in the reproductive processes of the Volvocales cannot be described here, but when they are discussed in a later chapter it will be found that in the method of sexual reproduction, as well as in structure, Pleodorina and Volvox are more complex than Pandorina and Eudorina.

It is apparent from the study of higher animals that they are characterized by the development of relatively enormous numbers of somatic cells which bulk large in contrast to the smaller mass of reproductive cells. The germ cells of the metazoa are of two kinds, large and small. Since Pleodorina and Volvox have somatic cells and two kinds of germ cells, these organisms resemble the higher animals more than they do the protozoa. In fact, most zoölogists consider them to be metazoa in spite of the fact that their near relatives are undoubted protozoa (if they are animals at all). Pleodorina and Volvox cannot be regarded as in the line of descent of the metazoa, but in form and in the degree of their differentiation they furnish excellent illustrations of primitive metazoa which possessed sterile and reproductive cells arranged in a single layer.

At the present time no living metazoa (unless Pleodorina and Volvox are considered metazoa) exist in which the cells of the adult are arranged in a single layer and in which there has been no differentiation of the somatic cells into several types. It can only be assumed that in the descent of the complex animals there were such simple metazoan ancestors. Beyond these simple forms there is a further gap, since in all the present-day metazoa the body consists of two or three layers of cells and these cells are of several or many different kinds. In the absence of animals intermediate between Volvox and the more complex metazoa just mentioned, the nature of the transition from one to the other can only be inferred by appeal to a principle known as the biogenetic law. This law can be fully illustrated only after an account of embryonic development is given, and is deferred to the chapter on classification of animals. It may be stated here, however, that according to the biogenetic law the evolutionary history of an animal is epitomized in its embryonic stages.

Blastula and Gastrula.—It is pointed out earlier in this chapter that metazoa arise from a fertilized ovum by repeated cell division. The cells thus formed adhere in a mass (Fig. 54) which in some animals is solid but in most of them is hollow. This hollow mass is called a *blastula* and the cavity in it the *blastocœle*. The blastula cells of certain species of sponges, starfishes and hydra-like animals develop cilia on their external surfaces, and soon thereafter the blastula bursts from the egg membranes and begins its existence as a free-living larva (Fig. 55). In other species it remains in the egg membranes until development has

proceeded further. Shortly after the blastula stage has been reached it is converted into an embryonic stage having two layers of cells. This conversion into a two-layered embryo is accomplished in various ways, apparently related to the amount of yolk (food material) which the egg contains. Since only primitive types of development can be expected to throw much light on very early evolution, and since primitive eggs presumably contained little yolk, only the blastulas derived from such eggs are here used in tracing the origin of the two layers. In some of the hydra-like animals the plane of division of some of the cells of the blastula (Fig. 56) is such that some of the daughter cells pass into the blastocœle. This process may continue until the entire blastocœle is filled. In a larger number of embryos the cells of the lower pole of the embryo invaginate (are folded in) to form an embryo, the *gastrula*, having two cell layers and a new cavity (Fig. 57) different from the blastocœle. The outer layer of cells is the *ectoderm*, the inner one the *endoderm*, the new cavity the *archenteron*, and the opening through which the archenteron communicates to the exterior is the *blastopore*. The blastopore is usually at first a wide opening which is soon reduced in size by a rapid proliferation of the ectoderm. In early members of the evolutionary series the blastopore doubtless functioned as a mouth and the archenteron as a digestive cavity. In certain species these organs retain their primitive functions but in others the blastopore may have a different fate. The endoderm, in all cases, retains its primitive nutritive function. In free-swimming gastrulas the ectoderm is ciliated and performs the functions of locomotion, protection, and perception of sensations.

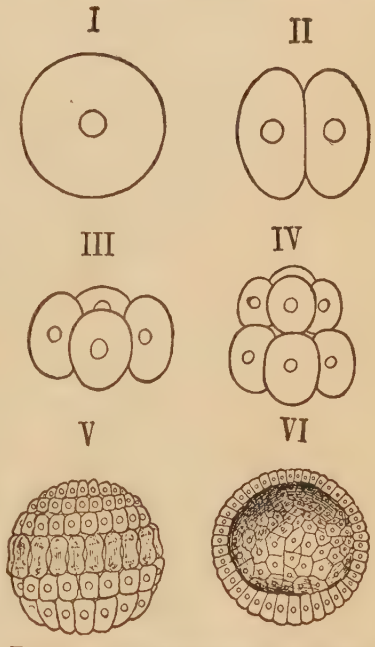

FIG. 54.—Early metazoan development. *I*, undivided egg; *II–IV*, further segmentation stages; *V*, blastula, exterior view; *VI*, blastula in section to show hollow interior or blastocœle. (*From Wilder's History of the Human Body, Henry Holt and Co.*)

The resemblance of the blastula stage, particularly of ciliated blastulas, to Volvox is striking; and the parallelism is strengthened by the fact that in some species of metazoan animals the earliest differentiation of cells that may be noted in the embryo is the differentiation of the somatic from the germ cells, a condition present in adult Volvox. In Sagitta, Ascaris, and some other species this visible differentiation occurs

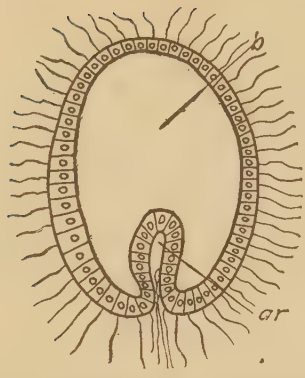

FIG. 55.—Gastrulation in the holothurian Synapta. *ar*, archenteron; *b*, blastocœle. (*From drawing by P. O. Okkelberg.*)

FIG. 56.—Embryo of medusa, Carmarina, showing endoderm cells being budded off into interior of blastula. (*Modified from MacBride's Textbook of Embryology, The Macmillan Co.*)

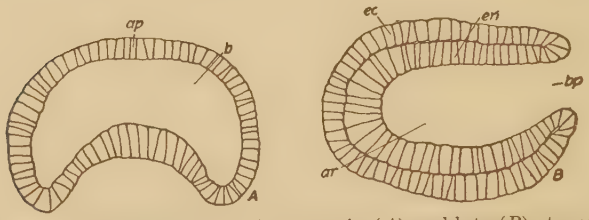

FIG. 57.—Formation of gastrula in Amphioxus, early (*A*) and late (*B*) stages. *ap*, animal pole; *ar*, archenteron; *b*, blastocœle; *bp*, blastopore; *ec*, ectoderm; *en*, endoderm.

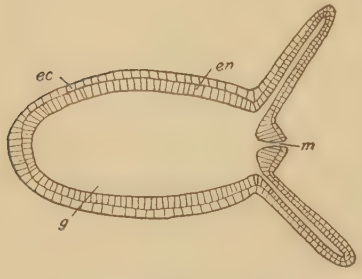

FIG. 58.

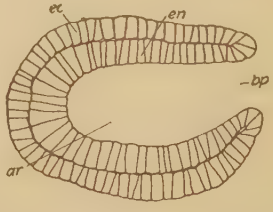

FIG. 59.

FIG. 58.—Diagram of longitudinal section of Hydra, for comparison with gastrula of typical metazoan animal, Fig. 59. *ec*, ectoderm; *en*, endoderm; *g*, gastrovascular cavity; *m*, mouth. The two body layers correspond to those of the gastrula and are similarly named; the gastrovascular cavity is equivalent to the archenteron; and the mouth corresponds to the blastopore.

FIG. 59.—Gastrula of Amphioxus. Compare with Fig. 58, a longitudinal section of Hydra. *ar*, archenteron; *bp*, blastopore; *ec*, ectoderm; *en*, endoderm.

very early. In other species it perhaps occurs as early but there is nothing about their size, form, or internal organization to distinguish somatic from germ cells until a later stage.

Animals with two cell layers like a gastrula exist at the present time. The bodies of Hydra, Obelia, and their allies are constructed of only two cell layers, ectoderm and endoderm. In these animals there is only one cavity, a *gastrovascular* (digestive) cavity with a single opening to the exterior. When the body of Hydra (Fig. 58) is compared with the gastrula (Fig. 59) it is evident that Hydra in its fundamental plan is a gastrula. It has, however, undergone certain modifications from the simple gastrula. These modifications are chiefly in the form of the body and in the degree of differentiation and specialization of its cells. As in other metazoa the mass of somatic cells greatly outbulks the germ cells, which are hidden within the soma. The somatic cells give to the body its form, size, and other characters by which the species is usually identified.

Hydra.—The form of Hydra (Fig. 60) is essentially cylindrical when extended and more or less globular when contracted. Ordinarily the body is attached by one end, the *foot*, to a solid substratum. At the tip

Fig. 60.—Hydra, showing general form of body, with bud.

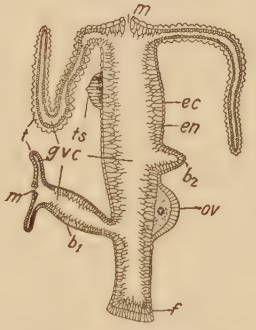

Fig. 61.—Hydra, diagrammatic representation of a sagittal section. *b*1, *b*2, buds in different stages of growth; *ec*, ectoderm; *en*, endoderm; *f*. foot; *gv c*, gastrovascular cavity or cœlenteron; *m*, mouth; *ov*, ovary; *t*, tentacle; *ts*, testis.

of the free end of the body the *mouth* is located. Near the mouth is a circlet of long contractile *tentacles* which have arisen from the body by an outpushing of the body wall. By means of the tentacles Hydra captures and thrusts into its mouth minute aquatic animals. The conical eminence between tentacles and mouth is the *hypostome*.

The gastrovascular or digestive cavity of Hydra (Fig. 61) is morphologically equivalent to the archenteron of the gastrula. It is sometimes called the *cœlenteron*, a name which gives rise to the word *Cœlenterata*, the designation of the group of animals which includes Hydra and its allies. The cœlenteron is continued out into the tentacles

and is lined by flagellated endoderm cells. Digestion of large masses of food occurs in the cavity, but small fragments are ingested by the endoderm cells. Hydra has no anal opening.

The ectoderm of Hydra has undergone differentiation in various directions. Some cells, only slightly modified, are called *epithelium*. Some of these epithelial cells are drawn out at the basal end into long slender processes which serve at once for contraction and for the transmission of nervous impulses. The outer ends of the same cells are capable of receiving stimuli. Such cells are called *neuromuscular* cells. Between the bases of the epithelial cells of the body and tentacles are groups of small cells. These, because of their location, have been named *subepithelial* cells. From them, at intervals, highly modified and specialized cells called *cnidoblasts* arise. The cnidoblasts gradually move to the surface of the body. Before and during the period of migration each cnidoblast secretes within itself a pear-shaped structure with a long slender thread coiled within it. This structure with its thread is a *nematocyst*. The cnidoblast also develops a trigger, the *cnidocil*, which projects beyond the surface of the body. When the cnidocil is properly stimulated by contact with a small animal, such as a minute worm or a small crustacean, the nematocyst discharges its poisoned thread. When numbers of the poisoned threads penetrate the body of a small animal they cause paralysis and Hydra is able to engulf the animal as food.

Among the subepithelial cells in certain regions of the body occur undifferentiated germ cells. At certain seasons of the year, varying with the species of Hydra, some of these germ cells begin to develop and finally produce *eggs* and *spermatozoa*. The epithelial cells in the region of the developing germ cells become somewhat modified, and they, together with the germ cells, give rise to elevations on the surface of the body. Those elevations which contain spermatozoa have a characteristic form and are called *spermaries* or *testes*. They are usually located on the third or half of the body nearest the tentacles. An elevation containing one or more ova is called an *ovary*. Testes frequently occur in numbers of two to ten or more, but there is usually but one ovary at a time. The ovary is usually located nearer the foot of the Hydra than are the testes. In form the ovary varies with age, but at all stages of its development it can be distinguished from the testes.

In sections of the body of Hydra a thin layer of a non-cellular jelly-like substance, the *mesoglœa*, can be seen between the ectoderm and endoderm. Embedded in it are the neuromuscular processes of some of the cells of the epithelium. The mesoglœa of the jellyfishes and some other members of the Cœlenterata may become many times as thick as the ectoderm and endoderm combined, and in it may be found scattered wandering cells, sometimes called *mesenchyme*. In this respect these

higher forms of the Cœlenterata approach the condition found in the bodies of the higher metazoa which have three cell layers.

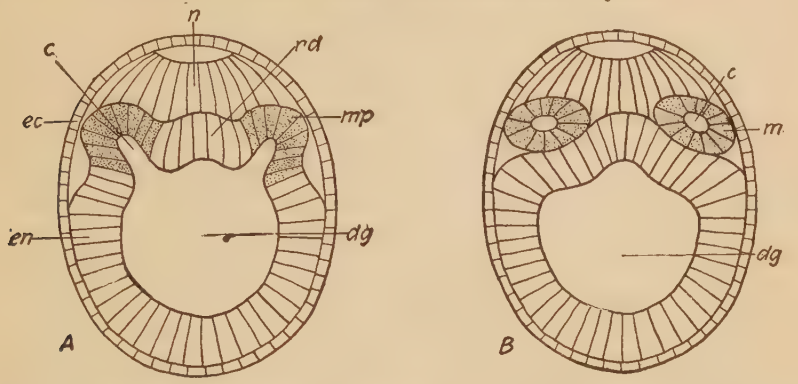

FIG. 62.—Mesoderm formation in Amphioxus. The endoderm (*en*) bulges outward into two ridges or mesodermal pouches (*A*, *mp*). These pouches become completely constricted off as tubes (*B*, *m*), which are the mesoderm and which contain a cavity (*c*), the cœlom. The other structures shown are: *dg*, digestive tract; *ec*, ectoderm; *n*, neural tube; *nd*, notochord. (*After Hatschek.*)

Well-fed hydras frequently reproduce by budding. In this process the two layers of the body in a restricted region fold outward and the cells in this area grow rapidly. When the bud has attained a certain size, tentacles are produced near the free end of the bud, and a mouth appears at the tip. On the third or fourth day from the beginning of the process the bud is usually large enough to support itself. It is then detached from the parent.

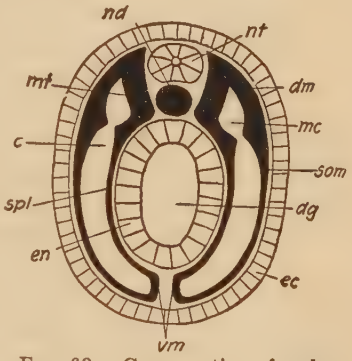

FIG. 63.—Cross-section of embryo of Amphioxus, showing expansion of the mesoderm between ectoderm and digestive tract. The mesoderm is shown in solid black, and is the same layer as the tubes (*m*) in Fig. 62. The mesoderm now consists of an inner or splanchnic layer (*spl*) and an outer or somatic layer (*som*), and also has thickened portions, the myotome (*mt*) and dermatome (*dm*). The cavity within the mesoderm, the cœlom (*c*), is specialized in the upper region as the myocœle (*mc*). The other structures shown are: *dg*, digestive tract; *ec*, ectoderm; *en*, endoderm; *nd* notochord; *nt*, spinal cord; *vm*, ventral mesentery.

The Third Layer of Cells.—All but two of the major groups of metazoan animals have progressed beyond the two-layered stage. These two exceptional groups are the Cœlenterata (hydra-like animals) and the Porifera (sponges). In all the other groups the body is composed of three layers of cells. The third layer is the *mesoderm*, which is developed between the ectoderm and endoderm. The method of formation of the mesoderm differs in different animals. In Amphioxus, a small marine fish-like animal (Fig. 89), the upper lateral portions of the endoderm bulge out in the form of two longitudinal hol-

low ridges, shown in cross-section in Fig. 62. The inner edges of each protruding ridge meet and fuse, and the hollow ridge is separated off as a tube. These two tubes are the mesoderm, and the openings in them are the body cavity, or *cœlom*. The tubes expand, enlarging the cœlom, one side of each tube becoming applied, as in Fig. 63, to the digestive tract, while the other side lines the ectoderm. The cœlom is thus entirely separate from the digestive cavity, and the presence of this additional cavity is an important distinguishing feature of the higher metazoa.

Derivatives of the Three Layers.—The three embryonic layers are called *germ layers*. From them all the parts of the bodies of metazoa are derived. The history of the three germ layers is similar in some respects in all the metazoa but there are many variations in detail, so that statements regarding the fate of the germ layers are not to be interpreted too rigidly. From the ectoderm arise the outer layers of the skin, and such structures as scales (in reptiles but not in fishes), feathers, hair, nails, and claws; the central nervous system, nerves, nerve endings, and sense organs which relate the animal to its environment; and some glands which discharge their secretions at the surface. From the endoderm arise the linings of the digestive tract and of the glands and other organs which arise from it by outfolding or evagination. In the vertebrates these derivatives of the digestive tract include the lining of the gill slits, the covering of the internal gills, the linings of the thyroid gland, lungs, swim-bladder, liver, and pancreas. The mesoderm usually gives rise to two main types of tissues which are characterized by the arrangement of the cells. These are mesenchyme, resembling the loose collection of cells called by the same name in jellyfishes, and *mesothelium*. The mesenchyme cells are at first wandering cells, and some of them retain this character, as, for example, the white blood corpuscles, pigment cells, and the red blood corpuscles. The last are confined within blood vessels. Some mesenchyme cells take up permanent positions in the body and secrete about themselves quantities of soft intercellular material. From these arise the inner layer of skin, the connective and packing tissues, and fat storage tissues. In certain positions the intercellular matrix, as it is called, becomes dense and stiff, and is called cartilage. This may become converted into bone. From the mesothelium arise the muscles, both striated and smooth, tissues of the heart and blood vessels, and the excretory organs and their ducts. It will be noted that in the vertebrate animals, at least, the mesoderm gives rise to a large proportion of the total mass of the animal. Without mesoderm the development of large bodies probably would never have occurred.

The germ cells are the undifferentiated lineal descendants of the fertilized ovum. They do not belong to any of the three layers but they congregate in the gonads, the supporting tissues of which are of mesoder-

mal origin. From the shelter furnished by the gonads the germ cells issue when mature.

Differentiation and Organization.—The foregoing account places much emphasis upon differentiation as an important process in the development of the soma and in making possible somas which are complex in structure and of large size. In the bodies of the higher metazoa, differentiation of somatic cells has been extensive and has resulted in a large number of kinds of cells. Those of each kind are usually grouped together in a plate or mass of varying size and form, and together perform a function common to all. Thus a specialized mass of epithelial cells may produce a certain secretion as their principal contribution to the physiological processes of the body. Other masses of cells may unite in contracting strongly on receiving an impulse conveyed by another group of cells. Such groups or masses of cells are called *tissues*. A tissue may be defined as a group of cells of the same kind coöperating in the performance of a function. The assumption of a special function, however, does not require cells to surrender all or perhaps any of their general functions; that is, the cells still respire, respond to stimuli, excrete and secrete, and they also perform within their cell bodies the hydrolytic and synthetic processes necessary to convert food materials into protoplasm or into their special cell product.

Tissues of different kinds are commonly very closely united with one another. Thus, tissues composed of epithelium are usually delicate, soft and easily torn, and are incapable of holding themselves in position because of lack of rigidity. These are almost without exception packed in, strengthened, and supported by various kinds of tissues derived from the mesoderm. If such a group of tissues is well delimited from neighboring tissues and has a special function to perform it is called an *organ*. An organ is an organization or association of tissues for the performance of a common function. In an organ there is always a principal tissue and accessory tissues. The stomach, intestine, the large intestine, and the rectum and other parts of the alimentary tract are organs. The larger *glands* (highly specialized secreting organs) such as the liver and pancreas are also called organs. Still further organization results when, as is usual, organs are associated in the performance of a general function. In the instance just cited the organs mentioned, together with certain others, all digest food or aid in that process. Each organ of the group performs one or more parts of the general function. An association of organs coöperating in the performance of a general function is called a *system* or *system of organs*.

Formation of Groups of Animals.—The differentiation referred to in the foregoing sections is described in generalized terms. This is possible because the processes of differentiation are, in their general features, much alike in nearly all animals. Tissues, organs, and systems arise

by the same general methods in all of them. In their details, however, the end products of differentiation present considerable variation, and as a consequence the external forms as well as the internal structures are of a variety of kinds. This variety is fortunately capable of being arranged in a limited number of large categories which removes much of the confusion which would otherwise result. Animals are thus easily arranged in a number of major groups, in each of which differentiation has produced forms that in some fundamental respects are alike. Upon this similarity of the results of differentiation rests the whole science of taxonomy, or the classification of animals. Full discussion of this classification is deferred until certain other foundation facts can be disclosed; but even at this point it is worth while to point out that differentiation goes beyond the formation of tissues, organs, and systems and produces these structures in a small number of characteristic ways. The groups of animals exhibiting these characteristic types of structure are known to the zoölogist as *phyla*, the principal ones of which are given with brief descriptions in the following synopsis.

Phylum Protozoa.—These are single-celled animals, mostly of microscopic size, though some are readily visible to the unaided eye. Many

FIG. 64.—Amœba.

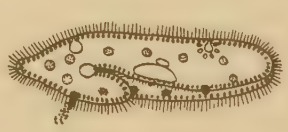

FIG. 65.—Paramecium.

FIG. 66.—Euglena.

species are colonial, but in these the cells are usually all potentially alike and no true tissues or organs are present. Spermatozoa and egg cells are usually lacking. Examples are Amœba, Paramecium, Euglena, Pandorina, and Eudorina (see Figs. 52, 53, 64, 65, 66).

Phylum Porifera.[1]—The bodies of these animals are always diploblastic (two-layered), and the body wall is penetrated by many pores. From this last fact the phylum takes its name. The animals possess a fundamentally radial symmetry, though this is often obscured by the tendency of the body to adjust its form to that of the object to which it is attached. The body wall is usually supported by a skeleton of spicules or of spongin fibers. Some of the water passages are lined with collared flagellate cells (Fig. 32). All members are aquatic, most of them

[1] This and the remaining phyla are composed of many cells, and are therefore called metazoa. This term is convenient when it is desired to contrast these phyla with the Protozoa, but it is not the name of a phylum and has no place in the classification of animals.

marine. The freshwater sponge and the bath sponge are good examples (see Figs. 67, 68).

FIG. 67.—A simple sponge. (*From Hegner's College Zoölogy, The Macmillan Company.*)

FIG. 68.—Elements of sponge skeletons. 1, spongin fiber surrounded by cells; 2–7, spicules of different types. (*From Van Cleave after Hertwig.*)

Phylum Cœlenterata.—These are diploblastic, radially symmetrical animals, provided with tentacles, stinging cells, a single gastrovascular cavity (cœlenteron), but no anus. Two body forms are prevalent, the polyp and the medusa. The phylum takes its name from the name of

FIG. 69.—Hydra.

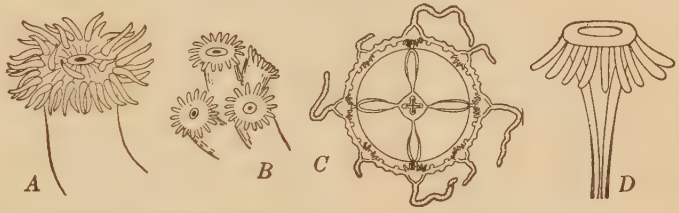

FIG. 70.—Various cœlenterates. *A*, sea anemone; *B*, group of coral polyps; *C*, medusa; *D*, hydroid polyp. (*A and B after Jordan, Kellogg and Heath; C after Mayer; D after Allman.*)

its digestive cavity, the cœlenteron. Examples are Hydra, Obelia, jellyfishes, sea anemones, and corals (see Figs. 69, 70, 154, 155, 157).

Phylum Ctenophora.—These are triploblastic (three-layered) animals, whose symmetry is partly radial, partly bilateral. The locomotor organs

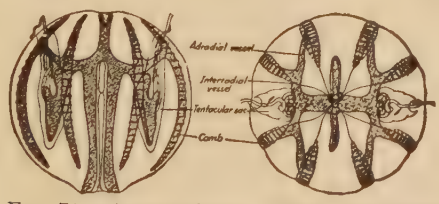

FIG. 71.—A ctenophore. (*From Van Cleave.*)

consist of eight rows of vibratile plates radially arranged. Sea walnuts and comb jellies are examples (Fig. 71).

Phylum Platyhelminthes.—These are triploblastic, bilaterally symmetrical animals, usually with flattened body. They may have a gastrovascular cavity without an anus, or in the degenerate parasitic forms like the tapeworms a digestive cavity is entirely lacking. The presence of a

cœlom is questionable. Animals of this phylum are commonly called flatworms. Examples are Planaria, flukes, and tapeworms (see Figs. 72, 73, 74).

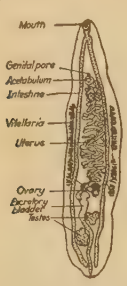

Fig. 72.—A fluke. (*From Van Cleave.*)

Fig. 73.—Planaria

Fig. 74.—A tapeworm.

Phylum Nemathelminthes.—These are bilaterally symmetrical, triploblastic animals with an elongated cylindrical body covered with a cuticle. A digestive tract with both mouth and anus is present. There is also a body cavity ("cœlom") surrounding the digestive tract. The

Fig. 75.—Hookworm. (*From Rivas, Human Parasitology, W. B. Saunders.*)

body is never segmented. Animals of this phylum are commonly called roundworms or threadworms, the latter word being the literal meaning of the name of the phylum. Some members of this group are well known parasites. Examples are Ascaris, Trichinella and the hookworm (see Fig. 75).

Phylum Echinodermata.—These animals are triploblastic. Their apparent symmetry is usually radial with five radial parts. They have a

Fig. 76.—A starfish.

Fig. 77.—A sand dollar. (*From Hegner's College Zoölogy, The Macmillan Company.*)

Fig. 78.—A sea cucumber. (*From Hegner's College Zoölogy, The Macmillan Company.*)

well-developed cœlom, a skeleton of calcareous plates and spines, and organs of locomotion (tube feet) operated by a water-vascular system. Common examples are starfishes, sea urchins, sand dollars, sea cucumbers, feather stars, and sea lilies (see Figs. 76, 77, 78).

Phylum Mollusca.—Members of this group present great diversity of structure. They are triploblastic, unsegmented animals with bilateral symmetry, but the symmetry is often obscured by a secondary spiral winding of the body. They possess a cœlom, and usually a shell. A structure called the foot, characteristic of the group, varies greatly in

FIG. 79.—A snail.

FIG. 80.—A clam.

FIG. 81.—A squid.

form. The common name mollusks refers to their soft bodies. Examples are snails, clams, mussels, oysters, cuttlefishes, squids, octopods, and the pearly nautilus (see Figs. 79, 80, 81).

Phylum Annelida.—These are triploblastic, bilaterally symmetrical elongated animals with external and internal segmentation. A cœlom is

FIG. 82.—Autolytus, a marine worm.

FIG. 83.—Æolosoma, a freshwater worm.

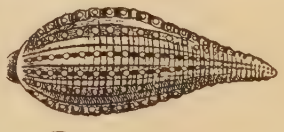

FIG. 84.—A leech. (*From Leunis.*)

present and setæ are common. These are the true worms. Examples are the earthworm, Æolosoma, Nais, Chætogaster, the sandworm, and leeches (see Figs. 82, 83, 84).

Phylum Arthropoda.—These are triploblastic, bilaterally symmetrical animals with segmented bodies made up of more or less dissimilar somites.

FIG. 85.—A crab. (*From Van Cleave.*)

FIG. 86.—A crayfish.

FIG. 87.—A beetle.

FIG. 88.—A centipede. (*From Hegner's College Zoölogy, The Macmillan Company.*)

The cœlom is much reduced. The appendages are jointed, and the skeleton is chitinous and surrounds the soft parts of the body. Examples are the crayfishes, shrimps, crabs, centipedes and millipedes, insects, and spiders (see Figs. 85, 86, 87, 88).

Phylum Chordata.—The animals of this phylum have at some stage a skeletal axis called the notochord, gill slits in the embryo or adult, and a nerve cord dorsal to the alimentary canal. (In preceding phyla when a nerve cord is present it is ventral to the alimentary tract.) This phylum includes a number of degenerate animals such as Balanoglossus and the tunicates which must be included here because of the presence of the

Fig. 89.—Amphioxus.

Fig. 90.—A fish.

notochord in the embryo. It also includes Amphioxus, a fish-like animal in which the notochord is the permanent skeletal axis. The other remaining chordates are called vertebrates from the fact that the notochord becomes invested with cartilage which becomes segmented to form a vertebral column. In some lower forms the cartilaginous vertebræ and the notochord which they surround persist throughout the life of the

Fig. 91.—A salamander.

Fig. 92.—A frog.

animal, but in the higher forms the cartilage is replaced by bone and the notochord disappears. Among the vertebrates are the lampreys and hagfishes, the sharks, skates and rays, the true fishes, the amphibians (salamanders, toads and frogs), the reptiles (lizards, snakes, crocodiles, and turtles), the birds, and the mammals (kangaroo, mouse, dog, horse, bat, whale, flying squirrel, the apes, and man) (see Figs. 89, 90, 91, 92, 172, 173).

CHAPTER VI

INTRODUCTION TO MORPHOLOGY AND PHYSIOLOGY OF HIGHER TYPES

Although morphology and physiology are by definition distinct subdivisions of biological science, it is impracticable to consider the structure of organs or systems adequately without reference to their functions, or to consider function apart from structure. Structure determines use, and use modifies structure.

In large part, the functions and structures are highly specialized. Systems of organs are devoted to specific performances, as is shown in the two succeeding chapters. There are, however, certain facts of morphology and certain types of function which are of general significance. They are related to various systems, or are scattered throughout the organism. The present chapter is devoted to these more general morphological features and widespread functions.

Symmetry.—Despite the great diversity of form existing among animals it is a striking fact that the members of most species exhibit some degree of *symmetry*. A figure which possesses symmetry may be divided by a line or plane in such a way that one half is a mirrored image of the other. If in such a figure any point be chosen on one side of the line or plane of division a corresponding equidistant point may be found on the opposite side. Animals which can be thus divided by a plane into two mirrored halves are said to possess symmetry while all others are *asymmetrical* (not symmetrical). The symmetry of animals is of three well-marked types, *bilateral*, *radial*, and *universal*.

Bilateral Symmetry.—Most animals of common acquaintance, as the dog, horse, fish, crayfish, clam and earthworm, possess a symmetry such that there can be only one plane which divides the animal into mirrored halves. Anterior (front) and posterior (rear) ends are different, and the dorsal (upper) and ventral (lower) surfaces are different, so that only the two sides are alike. In such animals the plane of symmetry must be passed through the antero-posterior axis of the body and through points on the mid-dorsal and mid-ventral lines. In this manner left is divided from right. Animals of this type with only two like sides exhibit *bilateral* symmetry, that is, two-sided symmetry.

Radial Symmetry.—Among certain groups of lower animals in which differentiation has not progressed as far as in the ones cited above, the form of the animal is almost a true cylinder or a modified cone. Ex-

amples of nearly cylindrical animals are to be found among the Cœlenterata, such as Hydra, jellyfishes, sea anemones, and most hydrozoan and coral polyps. A few of these are illustrated in Fig. 93. In all these animals, whether sessile or motile, the ends differ from each other. Hence a plane which divides the body into two mirrored halves must pass through the long axis of the body; but since the body is circular in cross-section and not differentiated into dorsal and ventral sides almost any plane which passes through the long axis of the body will cut it into mirrored halves. This type of symmetry is called *radial*. Ideally, if an animal is to exhibit radial symmetry it must be possible to pass an infinite number of planes through the long axis, such that each plane cuts the body into mirrored halves. Actual examples of such perfect radial symmetry are unknown and in practice an animal is regarded as radially symmetrical if two or more planes of symmetry are present. Thus in jellyfishes, because of the radial canals and some other structures,

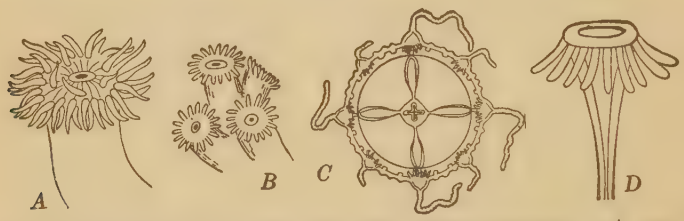

Fig. 93.—Various cœlenterates, showing their radial symmetry. *A*, sea anemone; *B*, group of coral polyps; *C*, the medusa, *Mitrocoma cirrata*, ventral view. *D*, polyp of the hydroid, *Perigonimus serpens*. (*A and B after Jordan, Kellogg and Heath; C after Mayer; D after Allman.*)

there are only four planes of symmetry. In Hydra (leaving out of account certain inconstant features) there are as many planes of symmetry as there are tentacles. The starfish is sometimes used to illustrate approximate radial symmetry, the number of dividing planes being five if five arms are present.

Universal Symmetry.—A few animals possess an approximate *universal* symmetry, but none show it perfectly. To exhibit universal symmetry it must be possible to pass planes through the body in any direction. Such planes must necessarily pass through a central point and the only geometrical solid which may be so cut is a sphere. Very few organisms, animals or plants, are truly spherical and most of those which are spherical exhibit polarity, that is, opposite sides are in some way differentiated, which makes their symmetry radial and not universal. Volvox, Eudorina, and Pandorina come as near universal symmetry as any animals which can be named, yet some species of Volvox exhibit a certain degree of polarity in that the germ cells tend to develop at one pole or on one side of the sphere.

Asymmetry.—Animals whose bodies cannot be cut by a plane into two mirrored halves are *asymmetrical.* Examples of asymmetrical protozoa are Paramecium, Amœba (in most states of motion), and Stylonychia. The snail with its coiled shell is asymmetrical but the body is built on a bilaterally symmetrical plan which has been subsequently modified by twisting.

Many animals which are externally symmetrical may have their internal structures arranged on an asymmetrical plan or on a plan of symmetry different from the external plan. Cases in point are found in the heart, stomach, and in fact the major portion of the alimentary tract and the lobes of the liver in man, which are arranged asymmetrically. Many animals which exhibit asymmetry in certain of their organs are symmetrical in early stages of development.

Symmetry and Locomotion.—An examination of a large number of animals in regard to their symmetry and a consideration of the mode of life employed by each animal, whether sessile, or capable of slow movement or of rapid movement, reveals a certain relationship between the type of symmetry and the character of locomotion. It is found that most animals which move rapidly or are capable of well coördinated direct movement exhibit bilateral symmetry. Examples in support of this statement are such mammals as the dog and horse, the fishes, amphibians, reptiles, the arthropods, most mollusks and most worms. A large proportion of animals of very slow movement, and those which are sessile, show radial symmetry. Examples are the cœlenterates, sponges, and some echinoderms,[1] especially the crinoids or sea lilies. Universally symmetrical animals are aquatic, and progress by a rolling motion.

Asymmetrical animals which have retained their powers of locomotion are relatively rare except among the protozoa. In many species whose individuals are apparently asymmetrical the asymmetry is due to modification of a fundamental plan of bilateral symmetry. The flatfishes, such as the halibut, flounder, and sole, which have two eyes placed on one side of the head, are in their early stages bilaterally symmetrical, but one eye migrates through the head to its new position. Asymmetry in adult parasitic crustacea is fairly common and is the result of degeneracy. Those species of crustacea, including some parasitic species as well as free-living ones, which retain their powers of locomotion are bilaterally symmetrical. The individuals of many parasitic species which are asymmetrical in either the adult or larval periods are always bilaterally symmetrical in their free-swimming stages.

[1] Frequent mention must be made, in this chapter, of the groups of animals. The information concerning the phyla given at the end of Chap. V will enable the student to visualize the animals sufficiently. Whether an animal is low or high in the animal scale is more important here than a knowledge of its appearance. Common names of members of the group may usually be found in the glossary.

Metamerism.—Animals exhibiting metamerism are composed of a linear series of body segments fundamentally alike in structure. These units are called *segments*, *somites*, or *metameres* and animals so constructed are said to be *segmented* or *metameric*. In simple metameric animals the somites closely resemble one another in size, form, and in the arrangement of organs. In no animal, however, are all somites entirely alike because some of them have become specialized and perform special duties. The common earthworm (Figs. 100, 145, and 148) is a metameric animal.

It is composed of a series of ring-like somites outwardly much alike. The limits of the somites are marked on the outside by grooves and on the interior by the septa (cross partitions), which lie immediately under the grooves. The segmental arrangement extends to both external and internal structures and involves organs of locomotion and excretion, muscles, blood vessels, and the nervous system. The sexual organs also have a segmental arrangement although they are limited to a few somites. Certain other organs are repeated in only a few segments, but in general the earthworm's structure is that of a metameric animal.

In complex animals the metameric arrangement has often become obscured through fusion of somites, loss of organs, and centralization. The primitive arrangement, however, is readily seen in the embryos of such animals. Thus the embryos of the vertebrates generally reveal a well-marked metamerism in certain organs (the muscles, for example), in which this arrangement is later partly or completely lost. Not all metamerism has been lost even in the adults of vertebrates, however, for in the mammals, for example, metamerism may be seen in the vertebræ, ribs (Fig. 118), spinal nerves and ganglia (Fig. 129), and branches of the dorsal aorta (artery).

Metamerism is interpreted by some biologists as indicating an ancestral colony formation, the somites representing the individuals of the colony. It is not improbable, however, that rhythmical processes occurring during development are responsible for the division of the body into similar parts, and that the ancestors of metameric animals were never colonial.

Cœlenteron and Cœlom.—The principal body cavities, *cœlenteron* and *cœlom*, have already been mentioned in the preceding chapter. The cœlenteron (Fig. 61) is the single cavity in the Cœlenterata (Hydra and its allies) which functions as a combined digestive and vascular cavity. It is, therefore, sometimes called a *gastrovascular cavity*, but the name cœlenteron is more expressive of its structural relations.

In many higher invertebrates and in the vertebrates there is, in addition to the digestive cavity, a second body cavity bounded by peritoneum lying between the gut and the body wall. This second cavity, the cœlom, is well shown in a diagrammatic cross-section of a

developing Amphioxus (Fig. 94). In the earthworm and in most other Annelida the arrangement of the body is clearly that of a tube within a tube. The wall of the outermost tube is the body wall while the alimentary tract forms the inner tube which is supported by circular partitions, the *septa*. The cavity (cœlom) between the walls of the two tubes is lined with the *peritoneum*, a layer of cells. In the vertebrates the inner tube is suspended from the inner surface of the outer tube by means of dorsal mesenteries which are merely continuations of the peritoneum from the mid-dorsal line. The relation of cœlom to intestine is illustrated in Fig. 95. In that figure the line limiting the cœlom represents the peritoneum. Figure 95 also clearly illustrates the fact that while the

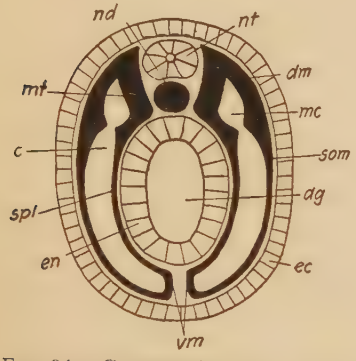

Fig. 94.—Cross-section of an embryo of Amphioxus, showing relation of cœlom to other structures. *c*, cœlom; *dg*, digestive tract; *dm*, dermatome; *ec*, ectoderm; *en*, endoderm; *mc*, myocœle; *mt*, myotome; *nd*, notochord; *nt*, neural tube; *som*, somatic layer of mesoderm; *spl*, splanchnic layer of mesoderm covering the digestive tract; *vm*, ventral mesentery.

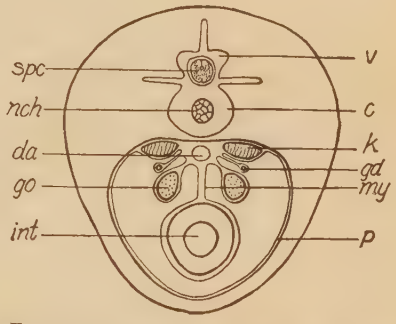

Fig. 95.—Diagram showing the relation of the cœlom to the intestine and other organs, and to the peritoneum. *c*, centrum; *da*, dorsal aorta; *gd*, gonoduct; *go*, gonad; *int*, intestine; *k*, kidney; *my*, mesentery; *nch*, notochord; *p*, peritoneum; *spc*, spinal cord; *v*, vertebra.

organs of the body really lie outside of the cœlom they are pushed down into it and are suspended by peritoneum. A true cœlom always bears the gonads on its walls and is lined with peritoneum. From the latter feature this cavity is frequently called the *peritoneal* cavity.

Internal Organization.—The organization of cells into tissues, tissues into organs, and organs into systems has been described in the preceding chapter. It is important, however, in relation to problems discussed later, to refer to the types of tissues and to describe in more detail sustentative and epithelial tissues, gland formation, and certain functions of glands.

Tissues may be classified with reference to their general functions into six types, *sustentative*, *epithelial*, *contractile*, *nervous*, *vascular* (blood and lymph), and *reproductive* (germ cells). All animal tissues may be referred

to one or another of these general types. The first two types are of general occurrence in many systems of organs, and are discussed below. The other four are more highly specialized, and accounts of them are deferred to later chapters in which the systems and processes to which they are most closely related are described.

Sustentative Tissues.—The sustentative tissues are all those which give support to the body and its parts, or connect and bind together cell layers, organs, and systems. They may take the form of rigid supporting tissues such as cartilage or bone; dense connective tissue such as tendons or ligaments; spongy, fibrous, or elastic connective tissues; or adipose tissue for storage of fat. In lower animals simpler types of rigid supporting tissues are found but they are omitted from this account. The sustentative tissues find their highest development among the vertebrates.

Occurrence and Function of Epithelium.—This kind of tissue covers all outer and inner surfaces of the body. It is composed of simple cells united by an intercellular cement to form a continuous surface. Examples of epithelial tissues in the earthworm are the hypodermis and intestinal epithelium, the peritoneum and chloragogen cells lining the cœlom, and the cells of the nephridia. In vertebrate animals the outer layer of skin, the inner linings of the entire digestive system including the secretory portions of the digestive glands (liver, pancreas, etc.), the peritoneum which lines the cœlom, the lining of all blood vessels and lymph channels of the body, the tubules of the kidney and the lining of the ureters and urinary bladder, the tubules of the gonads (reproductive bodies) or so-called germinal epithelium, and the linings of the passages of the reproductive system are made of epithelium. From this formidable list of organs, which is far from complete, the importance of epithelium may be judged.

Its functions in different situations are to protect exposed surfaces from abrasion and from noxious substances, and to carry on the processes of secretion, excretion, and absorption. Epithelial cells may also in simple animals and in some parts of highly differentiated animals receive stimuli and transmit impulses. Examples of epithelial cells which perform these functions are the neuromuscular cells of Hydra (Fig. 124, A), the olfactory epithelia lining the nasal passages, and cells in the taste buds of the tongue of vertebrates.

Types of Epithelium.—Epithelial tissues are classified with reference to the form and arrangement of their constituent cells, or according to certain structures which the cells may possess. Thus epithelial cells are called *columnar* if the height of the cells (thickness of the layer) is greater than their width (Fig. 96, *A*); *cubical* if these dimensions are nearly equal (*B*); or *squamous* (*C* and *D*) if the cells are very broad and flat and arranged like tiles in a floor. If the columnar epithelial cells possess cilia, or flagella, or protoplasmic collars and flagella, they are

designated, respectively, *ciliated* columnar (*E*), *flagellated* columnar (*F*), or *collared* epithelium (*G*).

The cells of the hypodermis of the earthworm and of the ectoderm of Hydra may be cubical or columnar depending upon the state of contraction of the animal. The cells of the tubules of the kidney of vertebrates are columnar or in some instances cubical. Examples of ciliated epithelium are found in the intestinal lining of the earthworm, the surface layer of the gills of mussels, the lining of the mouth and esophagus of amphibians (frogs, toads, and salamanders), the lining of the trachea and bronchi of air-breathing vertebrates, and the linings of certain ducts and passages of the genital system. Collared epithelium is found lining

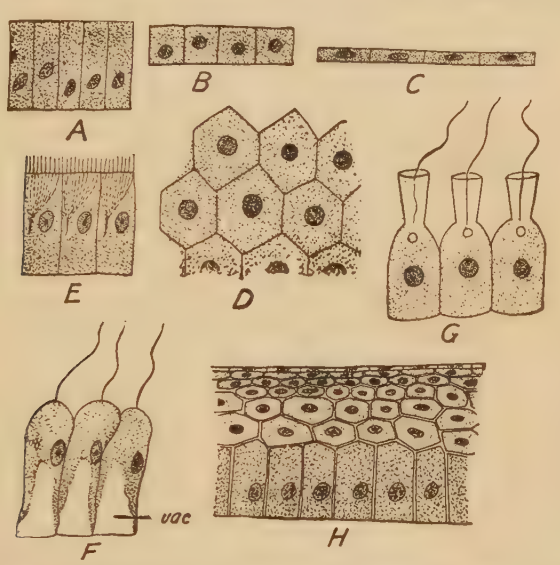

FIG. 96.—Types of epithelium. *A*, columnar; *B*, cubical; *C* and *D*, squamous (side and surface views, respectively); *E*, ciliated; *F*, flagellated; *G*, collared; *H*, stratified; *vac*, vacuole.

the radial canals of sponges (Fig. 32), while the endoderm of Hydra and other cœlenterates is composed of flagellated epithelium.

When the cells of columnar epithelium divide it is usually in a plane parallel to their long axis, that is, perpendicular to the surface which they cover. In this manner the layer remains one cell thick. In some situations, however, as in the outer skin of vertebrates, the mucous linings of mouth, rectum, and certain other organs, the columnar epithelial cells usually divide in a plane perpendicular to their long axis. The cells adhere after division and thus several layers of cells (Fig. 96, *H*) are built up and the epithelium is spoken of as *stratified*. The outer layers of cells in such epithelia become flattened until the outermost layer is composed of very thin flat cells which have the shape of polygonal tiles

(Fig. 96, *D*) accurately fitted together. Stratified epithelium forms the lining of the mouth and rectum of mammals and some other vertebrates. The outer skin of adult vertebrates is also made up of stratified epithelium. In the frog and other amphibians and certain reptiles, as snakes, the hardened outermost layer of skin (*stratum corneum*) is shed as an extensive layer. In most terrestrial vertebrates these outer cells are shed in minute flakes.

Glands.—Many epithelial surfaces are smooth or plain with all the cells lying in a single layer. In such a tissue scattered cells may be differ-

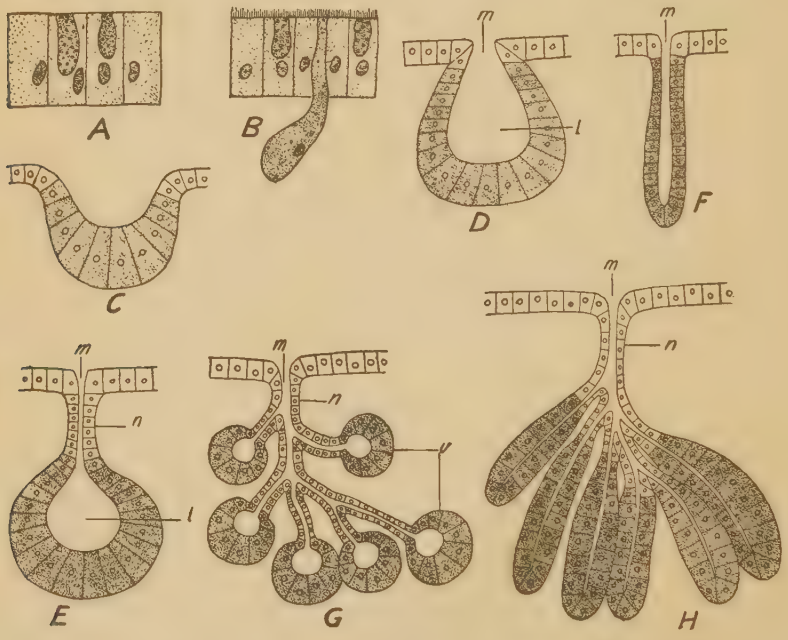

FIG. 97.—Types of secreting surfaces and glands. *A*, scattered gland cells (two goblet cells containing secretion in the darkly stippled *goblets*); *B*, gland cell enlarged and dropped below general level; *C*, group of secreting cells dropped slightly below the general level; *D*, a simple multicellular gland; *E*, alveolar gland with neck; *F*, tubular gland; *G*, compound alveolar gland; *H*, compound tubular gland; *l*, lumen; *m*, mouth; *n*, neck; *v*, acini. Secreting portions of the glands are stippled.

entiated from the others for the production of a secretion. The substance produced may be *mucin*, from which mucus is derived, some digestive secretion, or any one of many other products. Such a layer of epithelium is shown in Fig. 97, *A*, in which two goblet cells with their darkly stippled secretion are shown among columnar epithelial cells, and examples of it are found in the hypodermis of the earthworm and the intestinal epithelium of the frog. This is the simplest form which secreting surfaces may have. In slightly modified secretory epithelia the bodies of some secretory cells may be much enlarged and dropped

below the general level, as in Fig. 97, *B*. Examples of such enlarged and displaced secreting cells may be found in the epithelia covering the tongue of the frog and the foot and mantle of freshwater mussels. In other instances the secreting cells may be grouped instead of isolated, in which case they form what may be called a surface gland, as in *C*. A greater secreting surface is secured when a group of secretory cells drops below the general surface as in *D*. This constitutes a *simple* gland, that is, one which consists of a single depression and is not branched. It is produced by a process of *invagination* or infolding and may be *tubular* (Fig. 97, *F*) or *alveolar* (*D* and *E*) depending on whether the channels are of uniform bore or are inflated. If the invagination is carried far below the general surface, a *neck* (*E*) may be produced through which the secretions are conducted to the surface. The neck is usually composed of non-secreting cells. Glands of this sort are common in the skin of amphibians. Examples of tubular glands (*F*) are the sweat glands in the skin of man, the gastric glands in the stomach of the frog, and the glands situated between the bases of the villi in the intestines of mammals.

From a simple gland, as shown in Fig. 97, *E* or *F*, a *compound* gland may be formed, as in *G* or *H*, by secondary invaginations from the original invagination. Compound glands are common in the wall of the esophagus of mammals and certain amphibians. In the proventriculus (first division of stomach) of the chicken or pigeon are large compound glands.

It is not uncommon that glands produce two or more secretions. If so, there are usually as many kinds of cells as there are secretions produced. When stained, the different types of cells can usually be distinguished by their form and appearance. Glands producing two secretions are to be found in the cardiac end of the frog's stomach, and the pancreas produces three secretions.

Glands may be of microscopic size or they may be large. Examples of large glands are the spleen, pancreas, kidneys, and liver. The large size of these organs is not due entirely, however, to the amount of secreting tissue present, for most large glands as the liver and kidneys are composed of several kinds of tissue in addition to the epithelium. The additional portions include connective tissue, blood vessels, and nerves. These tissues have only an accessory function, for in each case the secreting tissue is epithelium. Some glands, for example, the mammary glands, may also owe part of their size to the secretion contained in them.

In view of the morphology of secreting organs, as described above, a gland may be defined as a structure which is derived from an epithelial surface and whose function is the production of a secretion or an excretion.

Secretion.—Every cell produces substances which are later used. The elaboration of these substances is called *secretion* and the substances elaborated are known as *secretions*. Unicellular organisms use most of their secretions within the cell, as is true also of a large number of

cells of multicellular organisms; but there are cells (those of glands) which discharge their secretion. A secretion which is discharged may perform its functions within a cavity of the body or may pass from the body. Since excretions also may be discharged from the body, or in plant cells may remain within the cell, it is not always easy to distinguish secretions from excretions. In general, excretions are of no further value, while secretions perform some function for the organism.

The Process of Secretion.—Secretion occurs within a cell as a result of the chemical activities of the general protoplasm, or perhaps of certain specialized structures within it. While the cytoplasm directly performs the function of secretion, there is much evidence, coming from experiments on regeneration, that cells which have been deprived of their nuclei do not secrete properly. This failure to carry on secretory syntheses in the absence of the nucleus has been explained by one investigator by the assumption that the nucleus controls the rapid oxidative processes of the cell. It is known that the process of secretion requires considerable energy which is derived from oxidative processes. The earliest visible traces of secretions are usually found near the nucleus as minute granules or droplets which later move to the periphery of the cell or to the region of discharge. Beyond these few facts little is known with certainty regarding the process of secretion.

Mode of Discharge.—Secretions are discharged from the cell in various ways. A common mode is diffusion of liquid secretions through the cell membrane. The secretions of the pancreas, liver, and gastric glands, and of some of the ductless glands, escape from the cell in this way. In some of these glands the secretions are stored within the cell in granules which are changed to fluid form shortly before discharge. Some secretions, such as oily secretions, and mucus which is produced in mucous cells in the form of mucin, are not diffusible. Mucin is discharged through the open ends of the *goblet cells*, so called because of their shape due to the enclosed mucin, or from other scattered cells which produce it. In mucus glands the thin cytoplasmic border of the cells which are inflated with mucin breaks down, thus permitting the escape of the secretion. Cells producing oily secretions may break down at their free ends, or in some instances the whole cell may disintegrate at the time of releasing the secretion.

In many glands the secretion is discharged from the cells and is retained in a dilatation of the lumen of the gland until the secretion is required. When the gland is stimulated in the appropriate manner the secretion is poured out as a result of contraction of the muscles of the gland. In many other glands the secretions are retained within the cells and are not discharged until the gland is stimulated. Stimuli which rouse glands to activity are of various sorts, the chief of them being nervous and chemical (by means of hormones). The action of a hormone

is exemplified by the stimulation of the pancreas and liver by secretin, as described later in connection with digestion. Control by the nervous system is discussed in a later chapter.

Glands of Internal Secretion.—Certain glands have no ducts and their secretions must diffuse (or empty) into the lymph and blood. These are called glands of *internal secretion*. In this category may be included the pituitary, thymus, thyroid, and adrenal glands. Some of the glands provided with ducts also produce one or more secretions that are absorbed by the blood and so these glands must be regarded as glands of internal secretion. These are the pancreas, liver, and sexual glands. The last mentioned glands maintain the germ cells, but they also produce some secretions which are absorbed by the blood and have a most profound influence upon physical and mental processes. The functions of some of these glands of internal secretion are coming to be known through experiments with removal of the glands and with feeding the extracts of glands. Some of their secretions influence blood pressure; others affect muscular contraction and muscular tonus; others control the growth of skeletal parts and of tissues, the growth of primary and accessory sexual organs and development of secondary sexual characters; and some influence nutrition and other metabolic activities. A study of internal secretions figures largely in the training of the medical investigator, but a further discussion of them would be too involved for this book.

Diversity of Glandular Secretions.—A considerable number of secretions have already been named and something of their functions pointed out, but they form only a beginning of the list that might be given. Among the secretions that may not immediately occur to the student as belonging to this class of substances are the sebaceous materials which make the hair and skin oily, milk for nourishment of young, wax such as beeswax, poisons like those of snakes and certain insects, acids such as formic, sulphuric, and hydrochloric, gas as in the swim bladder of fishes and the float of the Portuguese man-of-war, the ink-like sepia which is thrown out to cover up the escape of the cuttlefish, silk of silkworms and other insects and of spiders, the odors of insects by which they attract the members of the opposite sex, and the disagreeable odors of certain insects and mammals by means of which they repel other animals.

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CHAPTER VII

PHYSIOLOGY OF MAINTENANCE

The means of growth and repair of the animal body, and of obtaining energy for doing work, are secured through the digestion and utilization of food. The chemical transformations which go on in the body result in the production of waste materials which must be eliminated. Although all organs are doubtless involved in these processes, four systems, the digestive, respiratory, circulatory, and excretory are chiefly concerned. These systems are very closely related. Their functions merge at many points. One system can perform its function only in so far as it coöperates with one or more of the other systems. Owing to this important unity of action, these four systems are here discussed in a group. The simplest approach to them is through the organs of digestion.

Simplest Digestive Apparatus.—Since in the protozoa and sponges digestion is intracellular no digestive system or digestive organ can be said to exist. The most primitive multicellular digestive organ occurs in the simple cœlenterates. The gastrovascular cavity of Hydra may be taken as an example. In this animal (Fig. 61) the digestive organ consists of a simple bag whose wall is composed of flagellated epithelial cells. Branches of the bag extend out into the tentacles and into the buds if the latter are present. A single opening, the *mouth*, leads into this cavity. The cœlenterates in general have a digestive organ of this type and few modifications are shown. In none of them is there a second opening, the *anus*, through which indigestible materials may be voided to the exterior. The digestive apparatus of the cœlenterates thus consists of a single organ, and can hardly be called a system.

Digestive Systems in the Invertebrates.—Among the flatworms (Platyhelminthes) a true digestive system may be found. In the rhabdocœle turbellarians (Fig. 98) it consists of a mouth, a short *pharynx*, and a sac-like *intestine*. In the triclad turbellarians, the intestine (Fig. 99) is branched into three main parts of which one extends forward and two backward to the extremities of the body. These main branches have secondary branches which extend laterally toward the periphery. In the roundworms (Nemathelminthes) the digestive system consists of a straight tube which extends through the length of the body from the mouth to a posterior opening, the anus, through which undigested material is voided. In some species tooth-like structures may be developed in the mouth cavity, and muscular swellings may be present in the

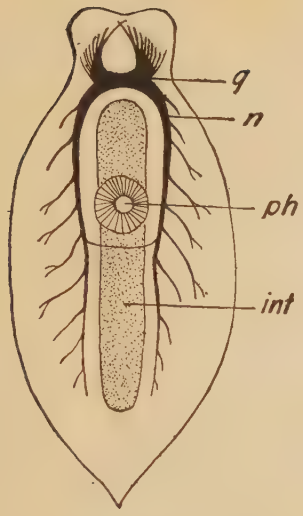

FIG. 98.—Digestive and nervous systems of a rhabdocœle turbellarian. *g*, ganglionic mass; *int*, intestine; *n*, nerve; *ph*, pharynx. (*After Lang.*)

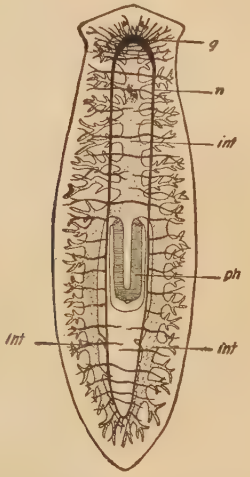

FIG. 99.—Digestive and nervous systems of a triclad turbellarian. *g*, ganglionic mass; *int*, intestine; *n*, nerve; *ph*, pharynx. (*After Lang.*)

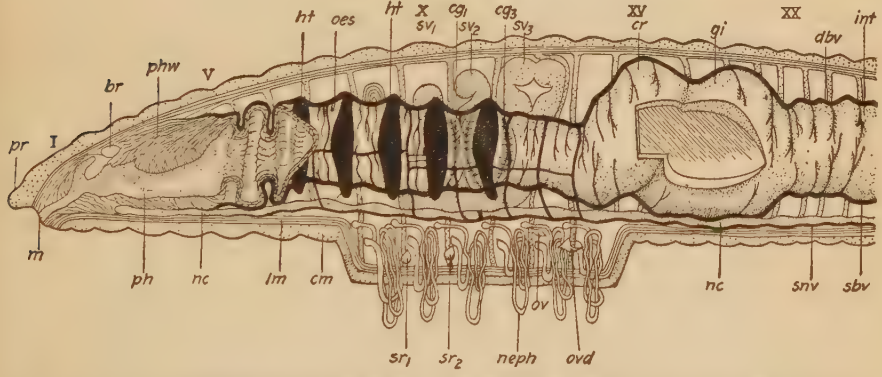

FIG. 100.—Dissection of the earthworm, *Lumbricus terrestris*, side view, showing various systems of organs. I, V, X, XV, XX, number of somite. Digestive system includes mouth (*m*), overhung by prostomium (*pr*), pharynx (*ph*), with thick muscular wall (*phw*), esophagus (*oes*), calciferous glands (*cg*1-*cg*3), crop (*cr*), gizzard (*gi*), intestine (*int*), anus not shown. Circulatory system includes hearts (*ht*), dorsal blood vessel (*dbv*), subintestinal vessel (*sbv*), subneural vessel (*snv*), and certain other vessels not here named. Excretory system includes nephridia (*neph*). Muscular system includes circular muscles (*cm*), longitudinal muscles (*lm*). Nervous system includes brain or supraesophageal ganglion (*br*), ventral nerve cord (*nc*), nerves not shown. Female reproductive system includes ovary *ov*), oviduct (*ovd*), seminal receptacles (*sr*1, *sr*2). Male reproductive system includes seminal vesicles (*sv*1, *sv*2, *sv*3), which enclose testes not shown, vasa deferentia not shown. For more complete diagram of reproductive system see Fig. 148. (*Modified from Linville and Kelly.*)

walls of the esophagus, but there is no differentiation into stomach and intestine. However, in one feature, the presence of two openings, there is an advance over all the digestive systems previously described.

The digestive system of the Annelida, of which the earthworm may be taken as an example, shows considerable differentiation into organs. It consists (Fig. 100) of a *mouth*, opening into a *buccal cavity*, a *pharynx* with strong muscular walls, an *esophagus*, a *crop* in which food may be stored, a *gizzard* with thick muscular walls and a chitinous lining by means of which food may be finely ground, an *intestine* with secreting and absorptive cells, and an *anus*. An internal ridge, the *typhlosole*, formed by an infolding of the dorsal wall of the intestine gives increased surface. About the exterior surface of the intestine is a layer of brown cells, the chloragogen cells, which have been thought to serve as a digestive gland, possibly as a liver.

Digestive Systems in the Vertebrates.—In the vertebrates the digestive system reaches its highest development. Here it consists not only of an alimentary canal, subdivided into regions, but also of highly developed glands which produce digestive secretions. The brief description below is based on the digestive system of the frog which is illustrated in Fig. 101.

The mouth, although it functions also in the respiratory processes, is to be regarded as part of the digestive system. The form of the mouth and mouth cavity is determined largely by the skeletal features of the head. The upper jaw bears *teeth* which serve to hold the prey when caught. Attached to the anterior portion of the floor of the mouth is a prehensile *tongue* which is provided with many *glands* that produce a sticky secretion. The *buccal cavity* or *mouth cavity* leads backward into the short broad *esophagus* through a distensible opening, the *pharynx*. The esophagus leads into the muscular *stomach* which in the frog, as in most vertebrates, is a curved organ usually lying somewhat to one side of the middle line. The walls of both the esophagus and stomach are provided with highly developed *glands* which secrete digestive solutions. The stomach opens into the much coiled *small intestine* through a muscular valve, the *pylorus*. The small intestine of vertebrates is usually subdivided into three portions named, respectively, the *duodenum*, *jejunum*, and *ileum*. Of these the duodenum and ileum alone are recognized in the frog. These regions as a rule merge imperceptibly into each other, yet each shows certain characteristic structural features and each occupies a certain portion of the intestine. The duodenum receives the secretions of two large digestive glands, the *liver* and the *pancreas*. In the frog the secretions of these two glands are discharged through the *common bile duct* into the middle region of the duodenum. A reservoir, the *gall bladder*, attached to the liver and connected with the bile duct, serves as a storage place for the *bile*, one of the secretions of the liver. The small

intestine is connected at its posterior end with the *large intestine* which in the frog is subdivided into two portions, namely, the *rectum* and the *cloaca*. The term cloaca is used to designate that portion of the large intestine which is used as a common passage for undigested materials from the alimentary tract, for urine, and for reproductive cells from the urino-genital system. It occurs in a few mammals and in most other vertebrates. The large intestine opens to the exterior by means of the *anus*.

In the diagram of the digestive system of the frog (Fig. 101) the intestine (small and large) is indicated as a relatively short tube. This

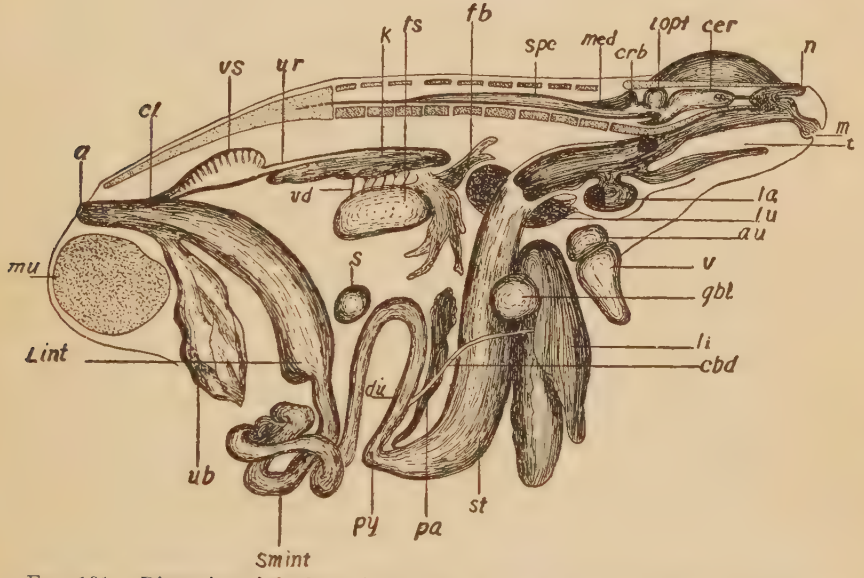

FIG. 101.—Dissection of the frog, side view. *a*, anus; *au*, auricle of heart; *cbd*, common bile duct; *cer*, cerebrum; *cl*, cloaca; *crb*, cerebellum; *du*, duodenum; *fb*, fat bodies; *gbl*, gall bladder; *k*, kidney; *la*, larynx; *li*, liver; *l. int*, large intestine; *l. opt*, optic lobe; *lu*, lung *m*, mouth; *med*, medulla oblongata; *mu*, muscle; *n*, nasal aperture; *pa*, pancreas; *py*, pylorus; *s*, spleen; *sm. int*, small intestine; *spc*, spinal cord; *st*, stomach; *t*, tongue; *ts*, testis; *ub*, urinary bladder; *ur*, ureter; *v*, ventricle of heart; *vd*, vasa efferentia; *vs*, vesicula seminalis. (*Modified from Parker and Haswell's Textbook of Zoölogy, after Marshall.*)

condition is found in flesh-eating animals in general. Animals which feed entirely or largely upon vegetable food have long intestinal tracts and frequently have a large *cæcum* (a blind pouch) at the junction of the small and large intestines. The rabbit and muskrat have a large cæcum with a *vermiform appendix* at its end; the chicken and dove have two cæca. In man the cæcum is small, rudimentary, with a vermiform appendix. Highly specialized modifications of the stomach occur in ruminants (animals which chew the cud) and in seed-eating birds.

Digestion in Man.—Inasmuch as the digestive process as it occurs in man has been much more intensively studied than in any other animal, the

discussion of digestion which follows will be based on the human system. In the mouth, food is broken up, during which process the three pairs of salivary glands pour out their secretion (*saliva*) which is mixed with the food. The saliva contains an enzyme, *ptyalin*, which is able to transform starch into certain sugars. This is not accomplished instantly, but the operation is much more rapid on cooked than on raw starches. The ptyalin first splits starch into *erythrodextrin* and *maltose*, one of the sugars. If time is allowed for the reaction the erythrodextrin is further acted upon, yielding maltose and another dextrin. This dextrin is broken down with somewhat similar results, and the final result of the action of ptyalin is that all of the starch is converted into maltose. Ordinarily, because of the short sojourn of the food in the mouth, little starch digestion actually takes place there, and since ptyalin acts only in an alkaline medium, its action is stopped by the acid of the stomach. The maltose remaining from salivary digestion is acted upon by inverting enzymes in the small intestine and associated organs, to which reference is made below. In the salivary secretion there is also some *albumen* and *mucin*. The latter is changed to mucus which acts as a lubricant for the particles of food.

In the stomach, the food is acted upon by the secretion of the gastric glands which are small branched or simple tubular glands located in the mucous layer of the stomach. The movement of the muscles of the stomach mixes the food with the gastric secretion, which contains *hydrochloric acid*, two important enzymes, *pepsin* and *rennin*, and perhaps a third enzyme of less importance, the gastric *lipase*. The hydrochloric acid affords a suitable medium for the action of the enzymes (except the lipase), and incidentally stops the action of the ptyalin descending from the mouth. The rennin coagulates milk, a fact made use of in cheese factories where a preparation of rennin made from calves' stomachs is used to separate the curd from the whey. Pepsin as it comes from the gastric glands is in an inactive state in which it is called *pepsinogen*. Pepsinogen is rendered active (converted into pepsin) by the hydrochloric acid, which is secreted in a concentration of about 0.4 to 0.5 per cent. The acidity of the gastric juice is usually estimated at about 0.3 per cent. Pepsin acts only on proteins converting them to peptones and proteoses. The process of absorption of the products of digestion through the gastric mucosa is not very active. Water and some sugar and peptones are absorbed, particularly if the solution be strong. Ordinary fats are not acted upon in the stomach, but emulsified fats (cream) are said by some investigators to be digested by the gastric lipase. A statement of the results of digestion of fats is deferred, however, to a later paragraph.

Secretin.—When the acid stomach contents are ejected through the pylorus, the acid acts upon a substance in the mucosa of the duodenum and changes this substance to *secretin*. The secretin is absorbed by the

blood and is carried to the pancreas and liver which are thereby stimulated to secrete their fluids. Secretin does not possess the characteristics of enzymes, since it is not affected by heat nor by alcohol; it belongs instead to a class of activators known as *hormones*. Normally, the pancreas and liver are also controlled in part by nerve impulses conveyed through the branches of the vagus and splanchnic nerves. Nevertheless, these glands discharge their secretions after the nerves which innervate them are cut.

The Pancreatic Juice.—The pancreas produces a thin watery secretion which amounts in quantity to about 500 to 800 cubic centimeters per day, or about 1 to 1¾ pints. This secretion contains three enzymes, which act upon proteins, carbohydrates, and fats respectively. The protein-splitting enzyme is inactive when it emerges from the pancreatic duct, and is then known as *trypsinogen;* but when it comes in contact with the duodenal surface it is quickly rendered active. This is explained by the assumption that the mucosa of the duodenum produces an enzyme, *enterokinase*, which reacts with the inactive trypsinogen changing it to an active form, called *trypsin*. The trypsin by hydrolysis splits proteins, proteoses, and peptones present in the chyme (partially digested food in a fluid condition) from the stomach into simpler and simpler compounds. As is to be expected from the composition of proteins, the end products of protein digestion are amino acids, of which about eighteen are known, and several other compounds. Trypsin works in alkaline, neutral, or even acid media. It completes the work begun by the pepsin, and works more rapidly and breaks up the protein more completely than does the pepsin.

The carbohydrate-splitting enzyme of the pancreatic juice is *amylopsin*. Unlike trypsinogen, it requires no activation. It produces a hydrolytic effect on starch very similar to that of ptyalin, producing maltose and a dextrin. These substances are further acted upon and converted into dextrose by an enzyme, *maltase*, secreted by the intestine. Dextrose is in condition to be absorbed.

The fat-splitting enzyme of the pancreatic juice is *steapsin*, sometimes called *lipase*. Steapsin by inducing hydrolysis splits fats into glycerol (glycerin) and one or more fatty acids of which fats are composed. The fatty acids combine with alkaline salts that are present in the food or are introduced by *bile*, the secretion from the liver, and soaps are produced. These soaps and uncombined fats become emulsified, that is, they become broken up into minute globules, and are finally completely hydrolyzed into glycerol and fatty acids. These substances are soluble and are absorbed in this condition. Steapsin is destroyed by acids, and works best when mixed with bile, which being alkaline, corrects the acidity of the food mass and assists in the emulsification and saponification of the fat.

The Secretion of the Liver.—Bile, the secretion of the liver, contains no enzymes. It contains water, bile salts, and certain excretory materials. The discharge of bile is stimulated by the hormone secretin in the same manner as is the secretion of pancreatic juice. Bile is ordinarily stored in the gall bladder until the acid chyme is ejected by spurts from the stomach. Each ejection of chyme is followed by an ejection of bile from the gall bladder. The bile assists the steapsin of the pancreatic juice in the digestion of fats. This action is considered to be due to the bile acids which serve as a solvent for fats and fatty acids. That bile is of importance in the digestion of fats is shown by the fact that if the bile is prevented from entering the intestine through the experimental formation of a biliary fistula a large share of the ingested fat is not digested and may be recovered in the feces.

The Intestinal Secretion.—The secretion of the small intestine is called the *succus entericus*. It is produced in small tubular glands which are local evaginations of the mucosa of the intestine. This secretion consists of *enterokinase*, *erepsin*, several inverting enzymes, and *secretin*. Enterokinase, as stated above, converts inactive trypsinogen into active trysin. Erepsin is a protein-splitting enzyme which acts particularly on peptones and deutero-albumoses, reducing them to amino acids and supplementing the action of trypsin. The inverting enzymes are three in number. These are *maltase*, *invertase*, and *lactase*. Maltase converts into dextrose the maltose and dextrins resulting from the operation of ptyalin and amylopsin upon starches. Invertase changes cane sugar to dextrose and levulose. Lactase converts milk sugar to dextrose and galactose.

Secretin, as indicated above in connection with the stimulation of the pancreas, is not an enzyme but a hormone. It exists in the mucosa of the duodenum as *prosecretin* which is stable and does not affect the pancreas. The acid from the gastric juice mixed with the food coming from the stomach changes the prosecretin into secretin which is absorbed and carried by the blood to the pancreas and the liver, which are thereby stimulated to secrete pancreatic juice and bile respectively.

Digestion in the Large Intestine.—The large intestine produces no enzymes. Water and some of the products of digestion are absorbed here. Bacteria flourish in the large intestine. Many of these attack proteins, while others attack the cellulose of plant cells and perhaps so break it down that some sugars are recovered from it. Bacteria which attack proteins are not numerous, however, when the products of protein digestion are rapidly removed.

Assimilation.—After foods have been converted into simple substances and rendered soluble they are absorbed. These substances are then resynthesized into more complex substances, that is, proteins, carbohydrates, or fats; or perhaps portions of them without being

recombined are oxidized with the liberation of energy. The method of synthesis is unknown but there is little doubt that enzymes play an important part in the process.

Absorption.—In the more complex animals absorption occurs along the portions of the alimentary tract. In such simple animals as Hydra all the endodermal cells are bathed in the products of digestion or carry on digestion in themselves, and through these cells absorption takes place. Some of this material not used by the endoderm is passed on by diffusion to the ectodermal cells unchanged, or possibly it is synthesized first in the endodermal cells, in which case the proteins, fats, and carbohydrates must again be broken down into diffusible substances before they are passed on to the other cells. In animals with a circulatory system, the simpler substances pass through the absorbing cells directly into the blood stream, or into the lymphatic system and then into the blood stream. The principles of osmosis, diffusion, and imbibition are usually invoked to explain absorption through the walls of the alimentary tract. Numerous experiments, however, conclusively show that absorption is often greatly modified by the activity of the absorbing cells.

Synthesis of Absorbed Substances.—During passage through the absorbing cells some of the simpler substances may be synthesized into more complex ones. This is certainly true of fats which are absorbed as glycerol and fatty acids, for these latter substances are not found as such in the blood stream nor in the lymphatics. Globules of fat can be demonstrated by proper staining methods in the epithelial cells of the intestine during the process of digestion, and after a meal the branches of the lymphatics which arise in the intestinal walls are white from the emulsified fat contained in the lymph.

There is still considerable discussion regarding the history of the amino acids after absorption. Recent investigations show that they are absorbed as such and that they occur in small quantities in the blood. It seems probable that they circulate in the blood stream and are selected as needed by the various organs for the synthesis of the particular proteins found in these organs. It is believed that some of the amino acids not used in the tissues are deaminized, that is, their NH_2 groups are removed, and the nitrogen is eliminated as urea, while the organic compound remaining may be oxidized, yielding energy.

The carbohydrates absorbed as dextrose or levulose are collected in the liver where they are transformed into glycogen, $(C_6H_{10}O_5)_x$, a substance having the same empirical formula as starch. This transformation is accomplished by means of enzymes. From time to time glycogen is released into the circulation as dextrose which is carried to the muscles and other tissues of the body where it is reconverted to glycogen and is finally used as a source of energy. In animals, glycogen may be synthesized from the products of protein hydrolysis and also from fats, especially from the glycerol portion of the fat molecule.

In animals, fats and carbohydrates are possibly used in the indirect synthesis of protein to a very limited extent, but plants are readily capable of such synthesis. In animals, the use of fats and carbohydrates effects a saving of proteins. Reserve fats are stored in fat-storing organs as the fat-bodies (*corpora adiposa*) of frogs and toads; in connective tissues between the skin and muscles, or between muscles; or about the abdominal viscera along the mesenteries. A small quantity of fat can be demonstrated in all the tissue cells where it occurs in minute globules.

The utilization of reserve foods requires the use of enzymes which occur in all the tissues of the body. These are *proteolytic*, *amylolytic*, and *lipolytic* enzymes, that is, protein-, carbohydrate-, and fat-splitting enzymes respectively. Many other enzymes, as *oxidases* and *reductases*, may also take part in these processes. How food reserves are built up into protoplasm is not known but it is supposed that enzymes are concerned in the process.

Conditions Necessitating Respiratory System.—The energy consumed in these syntheses and other metabolic processes is derived mostly from the oxidation of food and other substances in the protoplasm. Oxygen is required for this purpose. The larger the animal and the more rapid its metabolism, the more oxygen is used. The respiratory system must be such as to meet this demand. Special organs for respiration apparently arose much later than organs of digestion since they do not occur in the cœlenterates, rotifers, flatworms or roundworms, while digestive organs are present in these groups. Most Annelida (true worms) have no special respiratory system, nor do they require one since the moist mucous surfaces of their bodies serve the purpose of a membrane through which gaseous exchange may take place. In general the development of the respiratory system kept pace with the development of a circulatory system. In many small animals living in water or in moist environments, respiration may be carried on through the general body surface, and distributon to the cells may be effected by the diffusion. In such animals diffusion and modified osmosis may also be sufficient to carry digested foods from the place of digestion to the cells farthest from the digestive cavity. With increased mass of body, however, and with decrease of surface in proportion to mass, ordinary processes of diffusion of substances are not sufficient to meet the needs of the more distant cells. The difficulties arising out of the disproportion of mass to surface have been obviated by the development of a circulatory system, by which a fluid is taken round and round in a course leading past the digestive organs and in contact with moist membranes through which gaseous exchange may take place. In the presence of respiratory and circulatory systems the mass of the organism may be greatly increased. In fact, but for the development of these two systems, the size of animals

would of necessity have remained small and the efficiency of the organism limited.

Types of Respiratory System.—Respiratory organs are of three general types, namely, *tracheæ*, *gills*, and *lungs*.

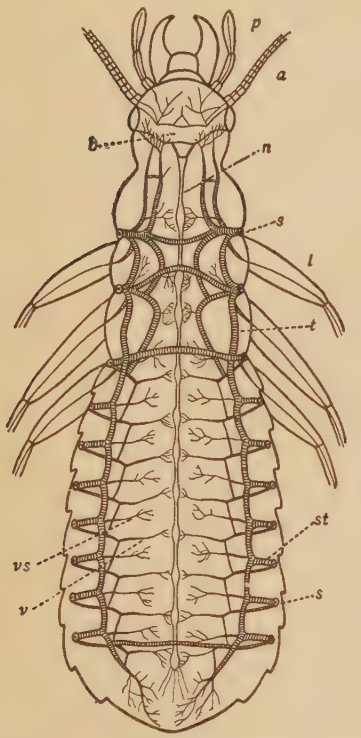

FIG. 102.—Tracheal system of an insect. *a*, antenna; *b*, brain; *l*, leg; *n*, nerve cord; *p*, palpus; *s*, spiracle; *st*, spiracular branch; *t*, chief tracheal trunk; *v*, ventral branch; *vs*, visceral branch. (*From Folsom's Entomology, after Kolbe.*)

TRACHEÆ. In most insects at certain points on the body are openings called *spiracles* to which are connected tubes, the *tracheæ*, which by their branches conduct air to all parts of the body. This type of respiratory system, which is illustrated in Fig. 102, is not dependent upon the circulation of an oxygen-bearing liquid to carry on the process of respiration, since every tissue is directly supplied with minute air passages through whose membranes gaseous exchange may take place.

GILLS. Gills are probably an earlier

FIG. 103.—External gills of the amphibian, *Epicrium glutinosum*. (*From Wiedersheim, after Sarasin.*)

and more fundamental type of respiratory mechanism than tracheæ since they occur in more primitive animals. Gills are to be considered as filamentous evaginations of an external mucous surface, or in fishes of the endodermal layer of the pharynx. Each filament is supplied with blood vessels which form a part of the circulatory system. Through the thin moist membranous walls of the gills gaseous exchange readily takes place. Gills occur only in aquatic animals or in terrestrial animals which have a method of keeping the gills moist. Examples of animals making use of gills are many polychæte worms, many mollusks, the crustacea, all fishes, and most amphibians in the larval state.

In vertebrates the gills are attached to cartilaginous or bony arches located in the region of the pharynx. There are slits between the gill arches through which water taken in at the mouth flows out over the gills. These arches and slits, in the embryo, are diagrammatically shown in Fig. 198 (p. 202). In fishes and some amphibians, a covering, the *operculum*, conceals and protects the gills, but in other amphibians, as Necturus and some other salamanders, the gills are external and are not covered. The external gills of a vertebrate are shown in Fig. 103.

A combination of tracheæ and gills (*tracheal gills*) is found in the aquatic larvæ of some kinds of insects, such as May flies, dragon flies, and certain beetles. In these larvæ the spiracles may be functionless or absent. Tracheal gills may occur on various parts of the body, as the thorax, the sides or end of the abdomen or within the rectal chamber.

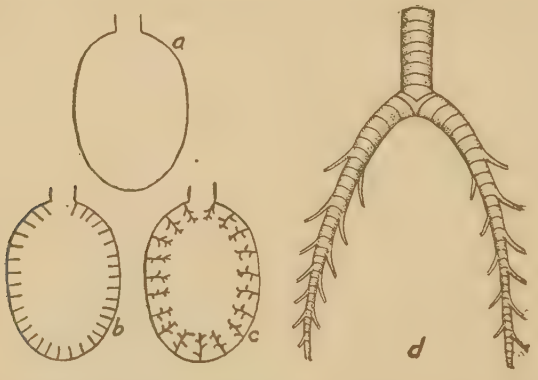

FIG. 104.—Diagrams of types of lungs. *a*, amphibian lung with plain surface; *b*, amphibian lung with low folds making simple alveoli; *c*, amphibian lung with higher folds which are themselves folded making more numerous alveoli; *d*, trachea and bronchial tree of a mammal.

These gills are richly supplied with tracheæ and are covered with delicate membranes which permit gaseous exchange.

LUNGS. Lungs are organs developed in the embryo of vertebrates as evaginations from the anterior end of the alimentary tract as described in Chap. XI. By means of accessory organs of respiration air is brought into the lungs where it comes into contact with mucous membranes richly supplied with blood vessels. Here exchange of gases takes place. In case of either lungs or gills the successful operation of the respiratory mechanism is absolutely dependent upon the continual changing of the blood in contact with the moist mucous surfaces. A halt in the flow of blood stops respiration promptly, and unless the flow of blood can be resumed death results.

The lung in lower amphibians is a bag-like organ with a large central cavity (Fig. 104); but in higher amphibians it becomes more complex since its inner surface is thrown up into corrugations with cross-corruga-

tions forming box-like spaces. These corrugations increase the respiratory surface. In higher vertebrates the lung is entirely subdivided into minute air spaces which are in direct connection with one another through large branching tubes, the *bronchi*. In this way there is an enormous increase of the inner surface of the lung. The bronchi unite in a single large tube, the *trachea*, which is present in the higher vertebrates, but absent in some of the lower forms, as the frog. The trachea opens into the mouth through a slit-like *glottis*.

Accessory Respiratory Organs.—Since in all vertebrates the mouth serves as a chamber for passage of water or air to gills or lungs, respectively, it may be considered a portion of the respiratory apparatus. For the same reason the olfactory passages of forms possessing lungs should also be included as a part of the respiratory apparatus. Located in the trachea or between the lungs and glottis is an organ of sound production, the *larynx*. This is a box-like structure in which are stretched two membranes, the *vocal cords*.

Relation to Circulation.—Since an essential part of the respiratory apparatus of animals with gills or lungs is the system of blood vessels with which it is richly supplied, and since the exchange of gases takes place directly through the walls of the blood vessels, the respiratory system is really subsidiary to the circulatory system. For an understanding of the process of respiration, therefore, an acquaintance with the circulatory system is first necessary.

Circulatory System.—The circulatory system is not present below the annelid and nemertean worms and mollusks. The essential feature of a circulatory system is a set of tubes which branch extensively so as to bring all parts of the body in contact with the circulating medium, *blood* or *lymph*. There is usually a contractile organ, the *heart*, or paired organs which by their rhythmic contractions serve to maintain a flow of the blood or lymph. The main distributing vessels are called *arteries*, the main collecting vessels *veins*, and the minute tubes leading from arteries to veins *capillaries*. In its course through the body the blood comes into intimate contact with the walls of the digestive organs where it secures dissolved food. It also comes in contact with the membranes of the gills or lungs where it takes up a supply of oxygen. The blood then carries this nutriment and oxygen out to all the tissues of the body and from them brings back to the lungs and the excretory organs carbon dioxide, urea, and other waste materials. In animals which have air tubes (tracheæ) the blood is a carrier primarily of nutriment and waste materials.

Chambers of the Heart and Course of Circulation.—The hearts of various vertebrates have two, three, or four chambers, and the course of the circulation is in part related to this feature of heart structure. A diagram of the circulatory system in the dogfish, an animal with a two-

chambered heart, is shown in Fig. 105. This diagram indicates that the blood of animals with gills and a two-chambered heart passes from the heart through the gills, and then out through the *dorsal aorta* to the organs of the body, where it passes through capillaries (not shown) and returns to the heart by means of the veins. The blood thus passes over a single course from the heart back to the heart again.

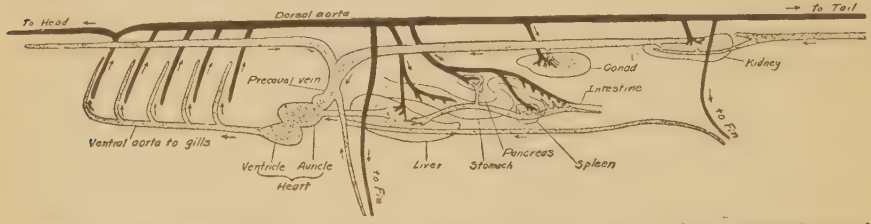

FIG. 105.—Diagram of the circulatory system in the dogfish. The capillaries and finer arteries and veins are omitted. (*Modified from Parker and Haswell's Textbook of Zoölogy.*)

In animals with lungs and a heart of more than two chambers the circulatory system is more complicated. The heart of amphibians and reptiles, except crocodilians, has three chambers in place of two as in the heart of fishes (Fig. 105), and the heart of mammals, birds, and crocodilians has four chambers. The four-chambered heart is composed of two halves, right and left. Each half is made up of two chambers, a thin-walled *auricle* and a thick-walled muscular *ventricle*. There is no passage between the two halves of the heart but there is a broad passage guarded by valves connecting each auricle with the ventricle of the same side. The relations of the parts of a four-chambered heart may be understood from Fig. 106, which also suggests the path of the blood.

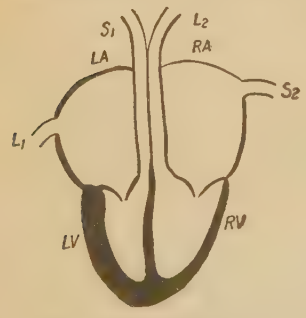

FIG. 106.—Diagram of a four-chambered heart. *LA*, left auricle; *RA*, right auricle; *LV*, left ventricle; *RV*, right ventricle; *L*1, vessel from lungs; *L*2, vessel to lungs; *S*1, vessel to system *S*2, vessel from system.

The blood of such an animal, after having made a circuit through the *systemic circulation* (through the body), is returned to the right auricle, whence upon contraction of the auricle it passes through a valve to the right ventricle. Upon contraction of the right ventricle the blood is sent through the pulmonary arteries to the lungs. Having completed the circulation of the lungs (*pulmonary circulation*) the blood returns to the left auricle through the pulmonary veins and from this auricle passes through the opening to the left ventricle. Upon contraction of the left ventricle the blood is discharged into the dorsal aorta whence it passes out to the systemic circulation. Upon its return it passes through the right side of the heart to the lungs, and so on around its course. The

circulation is thus a double one. The pulmonary and systemic circulations are kept absolutely distinct because the right and left chambers of the heart are completely separated from one another. In animals with a three-chambered heart, as in a frog, this distinctness does not prevail, for while there are two auricles there is but a single ventricle. There is therefore some mixing of the blood in the ventricle; but the structure of the ventricle with its deep recesses and the operation of valves in the principal artery are such that the mixing of venous and arterial blood is partially prevented.

Lymphatic System.—In addition to the system of vessels carrying blood in vertebrates there is a system which carries lymph and which is called from this fact the *lymphatic system*. It is composed of minute spaces between tissue cells which lead into thin-walled tubes, the *lymph vessels*. At intervals, connected with the lymph vessels, in some vertebrates, are contractile organs (*lymph hearts*) by whose contraction the lymph is forced along. The lymph vessels empty their contents into the venous system. In mammals they regularly connect with the left jugular vein.

Vascular Tissues.—Blood and lymph constitute the vascular tissues, as defined in the preceding chapter. Blood is composed of two parts, *plasma* and *blood corpuscles*. The plasma is a liquid, containing certain proteins, extractives, and inorganic salts. In the plasma float enormous numbers of blood corpuscles, of which there are at least three kinds, red cells (*erythrocytes*), white corpuscles (*leucocytes*), and *blood platelets*. Several kinds of leucocytes are recognized. Lymph is a fluid found in lymph spaces and lymph vessels. Its chemical composition resembles that of blood, from which it is largely derived. It contains certain kinds of white corpuscles, chiefly small *lymphocytes*, and rarely red corpuscles in small numbers.

Respiration.—It is largely through the agency of the blood and lymph that the process of respiration is effected. The oxygen requirement of living things is met by securing uncombined oxygen from the air or from solution in water. In most animals of any size and complexity tracheæ, gills, or lungs serve as respiratory organs. These organs present a surface large enough and of such a character that an ample supply of oxygen enters the tissues. In animals not so highly differentiated, or in some of those living in situations favorable to the maintenance of a moist external surface, the highly vascularized skin itself may function as a surface for gaseous exchange. This is particularly true of many of the annelid worms in which there are no gills, and of the frog and other amphibians in which the skin is an important organ of respiration. Any movements of the body or of its parts which tend to bring fresh air or fresh oxygen-laden water to these external or internal respiratory surfaces may be called *respiratory movements*. These movements in

terrestrial animals are ordinarily termed breathing. Respiratory movements also include the movements of the mouth and the gill covers of fish by which fresh water is circulated over the gills, and the movements of portions of the bodies of certain small aquatic annelid worms (Tubifex) which raise the posterior third or half of the body above the mud and wave it about in order to bring the skin in contact with more oxygen.

Mechanism of Oxygen Collection and Transportation.—In insects the circulatory system has little or nothing to do with the transportation of oxygen. Air enters the tracheal system through breathing pores (spiracles) on the sides of the body and is carried into the ramifications of the system by means of respiratory movements of the body. Oxygen in the minute tracheal vessels diffuses through the delicate membranes into the plasma with which the tissue cells are bathed and thence into the tissue cells. In most higher invertebrates and in the vertebrates, oxygen is transported by means of the blood contained in the circulatory system from the respiratory surfaces to the tissues of the body. Gills or lungs present a large surface for gaseous exchange. The internal surface of the human lungs has been estimated at more than 100 square yards, or many times the area of the body. Coming in intimate contact with the delicate membrane of the lungs or gills is the blood which is continually making a circuit through the circulatory system, as described below. The efficiency of the mechanism for oxygen absorption depends largely upon the properties of the protein *hemoglobin* which in vertebrates resides in the red blood corpuscles but which in most of the invertebrates having red blood is diffused throughout the blood plasma. Hemoglobin either adsorbs oxygen or readily enters into chemical combination with it, producing a compound known as *oxyhemoglobin*. Hemoglobin carries the bulk of the oxygen carried by the blood, a much smaller proportion of the oxygen being carried in solution in the plasma. Under normal pressure of oxygen in the atmosphere (equal to about 152 millimeters of mercury) hemoglobin is combined with oxygen (or adsorbs it) practically to saturation, and under higher pressure of oxygen no more is taken up. As the pressure of oxygen is reduced the oxyhemoglobin gives up some of its oxygen but the proportion lost is not great until the pressure of the oxygen is lowered to about 70 millimeters. Below this pressure it gives up its oxygen rapidly. Howell (Textbook of Physiology) states:

> The arterial blood enters the capillaries with its hemoglobin nearly saturated with oxygen—about 19 cubic centimeters to each 100 cubic centimeters of blood. After it leaves the capillaries the venous blood contains only about 12 volumes of oxygen to each 100 cubic centimeters of blood. In the passage of the capillaries, which takes only about one second, the blood loses, therefore, about 35 per cent or more of its oxygen. The physical theory of respiration furnishes data to show

that this loss is due to a dissociation of the oxyhemoglobin, owing to the fact that in passing through the capillaries the blood is brought into exchange with a surrounding medium—lymph, cell liquid—in which the oxygen pressure is very low.

Physical Theory of Respiration.—The movements of gases through membranes into tissues and liquids of the body or from these into the surrounding air or water is explained by the theory of diffusion of gases. If two volumes of gas, or two volumes of gas in solution, be separated by a permeable membrane, molecules of the gas pass through the membrane in either direction. If the tension or pressure of gas on one side of the membrane is greater than the other, a greater number of molecules of gas pass through the membrane toward the place of lower pressure than in the reverse direction. If permitted to do so the passage of molecules continues until an equal number of molecules is passing through the membrane in either direction; that is, until the pressure is the same on both sides. An equilibrium is thus established and the condition is the same as if no molecules were passing through the membrane.

In the air of the lungs or in the water bathing the gills the tension of the oxygen is greater than it is in the blood plasma or in the hemoglobin of the venous blood in the capillaries on the other side of the membrane. It has been estimated that in the lungs of man the tension of oxygen in the air of the alveoli is about 100 millimeters of mercury and the pressure of oxygen in the veins is 37.6 millimeters. According to the theory diffusion must take place from the place of higher tension to the place of lower tension. The blood is in constant circulation and the nearly saturated blood is borne away, blood poor in oxygen following in its place. The direction of diffusion of oxygen in the lungs is, therefore, always inward toward the venous blood.

It is estimated that in man the hemoglobin which reaches the capillaries out in the tissues is nearly saturated with oxygen, while the tissues and the lymph in which the cells are bathed are practically devoid of oxygen. Expressed in the usual way the tension of oxygen in the hemoglobin as it arrives in the capillaries is estimated at about 75 to 80 millimeters of mercury while in the tissues the tension of the oxygen is practically zero. Hence the oxygen rapidly diffuses from the blood plasma and the hemoglobin into the lymph and thence into the tissue cells where it is used in metabolism. The passage of the blood through the capillaries is estimated to require about one second; yet in this brief period of time the tension of oxygen in the hemoglobin is reduced from about 75 or 80 millometers of mercury to about 37.6 millimeters a loss in pressure equal to about 50 per cent. The blood plasma gives up practically all of its oxygen.

External and Internal Respiration.—From the above account it may be seen that respiration in animals that use a circulating medium for the transportation of oxygen to the cells resolves itself into two parts, namely,

the passage of the oxygen from the outside medium (air or water) into the blood, and the passage of oxygen from the blood into the tissue cells. These parts have been designated *external* and *internal* respiration, respectively. Internal respiration may be compared to respiration in Amœba, Paramecium or Hydra. External respiration is chiefly an accessory operation, loading oxygen upon the transportation system. The oxygen conveyed to the cells is consumed in the oxidation of carbohydrates, fats, and proteins, and other substances, a process which is accompanied by the release of energy, and the production of materials which cannot be used in the body.

Respiration is not readily separated, in one of its phases, from the process of excretion, or the removal of waste, since carbon dioxide is a waste material. The distinction is largely one of convenience in this phase. In so far as the materials eliminated in respiration are gaseous their elimination is regarded as a phase of respiration, but the wastes which are eliminated as liquids are excretions.

Carbon Dioxide Elimination.—A very small proportion of the carbon dioxide produced by the metabolic activities is discharged, in the mammals, through the skin in the secretion of the sweat glands; but in the frog a large proportion (in some species as much as 74 per cent) of the carbon dioxide may be eliminated through the skin. A small quantity is eliminated through the kidneys, but in mammals and most other air-breathing vertebrates the lungs are the most important organs for the elimination of carbon dioxide. The relative efficiency of gills and skin in aquatic forms with respect to carbon dioxide elimination is apparently not well established. The mechanism employed in carbon dioxide elimination from the tissues and through the lungs is about the same as that of the oxygen intake. The operation of the mechanism depends upon diffusion of gases. The tension of carbon dioxide in the tissue cells is greater than in the blood of the capillaries. This tension has been found by experiment in man to be about 50 to 70 millimeters of mercury in the tissues and about 35 millimeters in the arterial blood. Under these conditions the carbon dioxide diffuses from the cells into the lymph and from the lymph through the capillary walls into the blood stream. Here some of the carbon dioxide goes into solution in the plasma, some enters into chemical combination with sodium and potassium salts in the plasma and in the corpuscles, and some into chemical combination with the hemoglobin, or perhaps is adsorbed by the hemoglobin. The tension of carbon dioxide in the alveolar air of the lungs of man has been determined to be equal to 35 millimeters of mercury while that in the venous blood is 42.6 millimeters. As a result of this difference in tension the carbon dioxide diffuses through the membrane into the alveoli of the lungs. From the alveoli it is carried to the exterior with the exhaled air. The method of elimination of carbon dioxide from gills does not differ in its essential

features from the method outlined above. The quantities, however, are proportionately smaller.

Excretion of Water.—The oxidation of digested foods and the processes of metabolism in general lead to the production of waste substances. Water, used as a solvent and in an important way involved in chemical reactions, as in the hydrolysis of foods and the synthesis of various organic substances, is taken in in large quantities, and must be removed. It constitutes the most abundant of all wastes. In vertebrates, water is eliminated from the lungs, skin and kidneys, but the relative importance of these organs varies widely in different species. In the frog the elimination of water through the skin may be very great especially if the frog is in dry air. Under such circumstances the loss of water from the skin may be sufficient to kill the frog in a few hours. In the dog, which has no sweat glands except on the skin of the nose, very little water is eliminated through the skin, while in other mammals which perspire the elimination of water through the skin may be considerable. In man the quantity of sweat may amount to 2 or 3 liters per day, but is extremely variable. Sweat is secreted by the sweat glands, of which there are about two millions in the human skin. The lungs of man eliminate an appreciable quantity of water as water vapor but this quantity varies within narrow limits. In the dog, which eliminates very little water through the skin, the quantity of water eliminated by the lungs varies considerably being much greater when, because of heat or exertion, the dog pants. The kidneys are the most important organ for elimination of water. The quantity of water eliminated through them in man varies inversely with the quantity eliminated through the skin.

Excretion of Nitrogen.—Normal digestion of proteins in the alimentary canal gives rise to amino acids and some ammonia. Probably the hydrolysis of proteins in the protoplasm yields the same nitrogenous compounds. Some of the ammonia is eliminated in the form of ammonium salts and some of the amino acids in the free or combined form. The larger proportion of each substance, however, is first converted into *urea*. It has been established that urea is not formed in the kidneys, which eliminate it, but is formed in the liver and perhaps also in the tissues whence it is carried to the kidneys by the blood. Other sources of urea may be ignored in this account.

Excretory System.—The elimination of water and nitrogen waste is accomplished by very different systems in different animals. The simplest form of excretory system occurs in the rotifers, flatworms, and certain other low invertebrates, and consists of *protonephridia*, which are fine tubes rising in *flame cells* and discharging to the exterior. A portion of such a system is shown in Fig. 107, and the structure of a flame cell in Fig. 108. The flame cell is somewhat stellate or irregular in shape, hollowed out to form a funnel-shaped cavity within itself. A number of

long, slender cilia (the "flame") take their origin from the body of the cell and hang freely into the funnel-shaped cavity. In life, the cilia beat continuously and by their beating cause currents in the liquid which is excreted into the funnel by the cell.

Nephridia.—In the annelid worms each segment or somite (with some exceptions) is provided with a pair of more or less coiled tubes, the *nephridia*, which have a funnel-shaped ciliated opening, the *nephrostome*, which projects through the septum into the cavity of the somite ahead. There it opens directly into the body cavity or cœlom. The other end of the coiled tube is connected to the body wall where it has an opening to the exterior. The body of the nephridium in the earthworm, shown diagrammatically in Fig. 109, is composed of coiled tubes arranged in three distinct loops. The nephrostome sweeps in liquid and small solid particles by

Fig. 107.—Portion of a protonephridial system from the tapeworm *Tænia crassicollis*. *f*, flame cell; *n*, nucleus of excretory tubule; *tu*, excretory tubule. (*From Hesse and Doflein after Bugge.*)

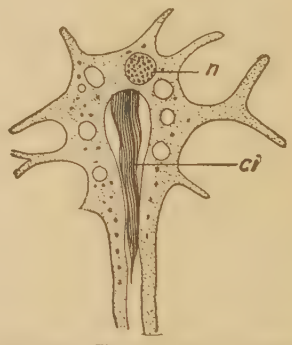

Fig. 108.—Flame cell of a protonephridium of a flatworm. *ci*, cilia within funnel-shaped cavity of flame cell; *n*, nucleus. (*From Hesse and Doflein after Lang.*)

the action of its cilia. A portion of the tube is also provided with cilia which assist in propelling liquids through the nephridium to the exterior. Other portions of the nephridium are composed of cells which have a secretory function. All parts are richly supplied with blood vessels.

Kidneys.—The excretory organs of vertebrate animals consists of large compact glands, the *kidneys*, which are made up of convoluted tubules (called *uriniferous tubules*) beginning in globular swellings, the *Malpighian corpuscles* (Fig. 110). The Malpighian corpuscle is composed

of two parts, the glomerulus and Bowman's capsule. The glomerulus consists of a group of blood capillaries surrounded by Bowman's capsule which is the expanded and invaginated end of one of the uriniferous

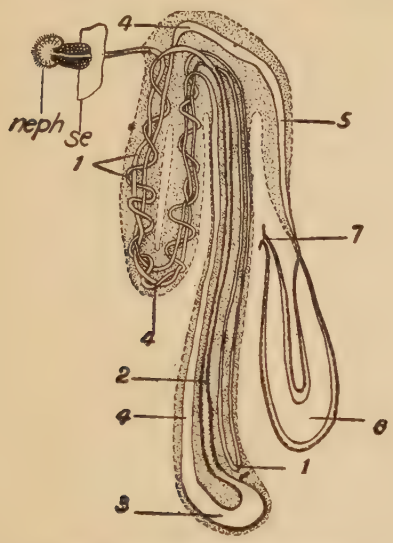

FIG. 109.—Nephridium of earthworm, schematic. *neph*, nephrostome; *se*, portion of septum; 1–6, portions of tubule of the nephridium; 7, opening to exterior. (*From Hesse and Doflein after Maziarski.*)

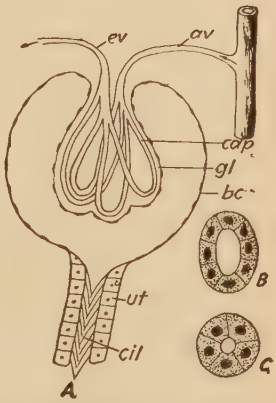

FIG. 110.—Structures from vertebrate kidney, diagrammatic. *A*, Malpighian corpuscle; *B* and *C*, cross-sections of uriniferous tubules at different levels; *av*, afferent vessel; *bc*, Bowman's capsule; *cap*, capillary; *cil*, cilia; *ev*, efferent vessel; *gl*, glomerulus; *ut*, uriniferous tubule.

tubules forming a double-walled cup. Each tubule consists of a single layer of secreting epithelium lying throughout its course in intimate contact with a rich supply of capillaries from the circulatory system.

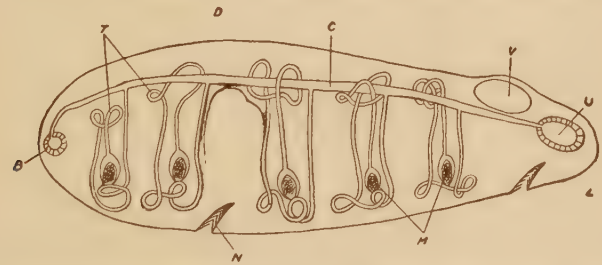

FIG. 111.—Diagrammatic representation of a cross-section of the kidney of a frog. *B*, Bidder's canal; *C*, collecting tubule; *D*, dorsal, *L*, lateral margin of kidney; *M*, Malpighian corpuscle; *N*, nephrostome; *T*, uriniferous tubule; *U*, ureter; *V*, renal protal vein. (*Modified from Holmes's Biology of the Frog.*)

In some of the lower vertebrates, as the lamprey and the frog, there are ciliated funnels or *nephrostomes* (Fig. 111) situated on the ventral surface of the kidney and opening into the body cavity. In the larvæ

of these species the nephrostomes connect the body cavity with the uriniferous tubules but in adult frogs the nephrostomes are connected with the blood vessels instead of with the tubules. A diagram of the structures found in the kidney of the frog is shown in Fig. 111.

The kidneys discharge into *ureters* which in turn discharge into the *cloaca* in lower vertebrates, as the frog, or into the urinary bladder in mammals. In the frog the urinary bladder is located on the ventral side of the cloaca but the ureters are not directly connected with it. Urine discharged into the cloaca by the ureters collects in the bladder and thence is discharged at times through the cloaca. The urinogenital apparatus of the frog is described in another chapter in connection with breeding habits. In mammals, except the few which have a cloaca, the urinary bladder is connected with the exterior by means of the *urethra*.

Relation of the Structure of the Kidney to Excretion.—The function of the kidneys is determined largely by the Malpighian corpuscles, and the uriniferous tubules with the adjoining capillaries, as described above. The uriniferous tubules (Fig. 110, *B* and *C*) are composed of more or less cubical or pyramidal cells which have a granular protoplasm. Near the Malpighian corpuscle the cells of the tubules, in lower vertebrates at least, are ciliated. The tubule may vary considerably in size in different parts of its length. The minute blood vessels of the glomerulus take their origin in an afferent blood vessel and discharge into an efferent arterial vessel. It is probable that no other organ of the vertebrate body is more richly supplied with blood than the kidney. In man it has been estimated that under the influence of diuretics (substances which cause increased flow of urine) the amount of blood flow to the kidney may in one minute equal the weight of those organs. This is said to be 4 to 19 times the average relative blood supply of other organs of the body.

Theories of Urine Elimination.—There are two principal theories as to the action of the parts of the kidney in elimination of urine. The earliest and simplest one of these theories, that proposed by Ludwig, is known as the *mechanical theory*. According to it, urine elimination, is explained by the *filtration* of water and dissolved substances, as salts, urea, etc., from the blood through the thin membranes of the glomerulus and the capsule. The urine according to this theory is dilute as it enters the tubules but is modified, during its passage through the tubule, by diffusion. The other theory, developed by Bowman and Heidenhain, asserts that water and certain salts are eliminated from the blood through the membranes of the glomerulus by an act of *secretion*, and that the urea and other organic compounds found in the urine are secreted by the cells of the tubules. Many experiments have been performed to test various phases of these two theories, but the results are not entirely in

harmony, and a complete understanding of the elimination of wastes in the kidney awaits the future.

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CHAPTER VIII

LOCOMOTOR SYSTEM AND NERVOUS CONTROL

Two of the most striking properties of animals are locomotion and response to stimuli. Movement of parts and locomotion from one place to another are accomplished by means of contractile portions of protoplasm in the protozoa, and by means of specialized contractile cells or tissues (muscles) in more complex animals. To perform these movements in large animals, supporting structures are required. These may be rods or spicules in the sponges; elaborate jointed exoskeletons in the arthropods; or articulated bones and cartilages held together by dense connective tissue in the vertebrates. The supporting or skeletal systems of the last two types furnish attachments for muscles, and become systems of levers by means of which locomotion is accomplished. The muscles and levers together comprise the locomotor system. Movement, locomotion, responses to stimuli from the outside world or from within the animal, glandular and other types of activities, in all but the most lowly metazoa, are induced, coördinated, and controlled chiefly by the nervous system. This system is composed of nervous tissues consisting of cells highly specialized for the reception of stimuli and conduction of impulses. The control exercised by the nervous system, while extending to all other systems, is most easily demonstrated in connection with the locomotor system. The two are discussed together in this chapter.

Contractile Tissues.—Under the term *contractile tissues* are included all tissues which by their contraction serve to produce movement of an organ or part, or locomotion of the animal as a whole. Among lower animals many individual cells, as the *porocytes* which control the size of the pores through which water enters a sponge, have the power of contraction. Such scattered cells do not form tissues.

Muscle.—In multicellular animals, while a large proportion of the cells are capable of slight contraction, certain cells are highly developed for purposes of contraction. Those cells in the metazoa which have developed within themselves fibrillar structures capable of great contractility are *muscle cells*. Muscle cells rarely occur singly in organs or tissues but usually as plates or bundles called *muscles*. Two types of muscle cells may be recognized. Cells of one of these kinds are simple in structure, capable of only relatively slow contraction; those of the

other kind are complex and are capable of rapid contraction. The former are known as *smooth* muscle cells and the latter as *striated.*

Smooth muscle is composed of cells each of which is provided with a nucleus. The cytoplasm contains well-marked longitudinal fibrils. These cells (Fig. 112) have the form of slender spindles with unbranched tips or in certain organs the tips may be branched. They are capable of strong but relatively slow contraction and are slow in relaxation. In higher animals they occur in organs in which rapid contraction is not required, for example in the walls of the digestive tract, urinary bladder, gall bladder, arteries and veins, and in certain glands and their ducts. Often these cells are arranged in layers which are applied to the organs in different directions, as transversely and lengthwise, respectively, giving rise to *circular* and *longitudinal* muscles. Smooth muscle is under the control of lower nervous centers and is therefore not directly subject to the will. For this reason it is sometimes called *involuntary* muscle. Striated muscle, except heart muscle, is under the control of higher nervous centers, and since its contraction may be initiated by an act of the will it is called *voluntary* muscle.

FIG. 112.—Smooth muscle cells.

Striated muscle differs from smooth muscle in the character of its fibrillæ which are striated and in respect to the number of nuclei within the cell. Striated muscle, except the heart muscle of the vertebrates, is composed of much elongated parallel cells each containing numerous nuclei which are scattered among the fibrillæ. Striated muscle cells originate from undifferentiated cells each of which has a single nucleus, but after a time division of the nucleus is not followed by division of the cell. As a result the cells become very large and they have many nuclei. The fibrils which are not present in the very young cells are elaborated in their further development. In the adult muscle (Fig. 113) one may recognize that the separate cells or fibers are surrounded each by a dense tough sheath, the *sarcolemma.* Within the sarcolemma are a large number of fine fibrillæ scattered through the cytoplasm. The cytoplasm of muscle cells is usually called *sarcoplasm.* The fibrillæ, also called *sarcostyles,* are composed of bands of material which present the appearance of alternate dark and light cross stripes. The structure of the sarcostyles may best be seen in cells which have been gently torn to pieces with fine needles. Figure 113, *C*, illustrates diagrammatically the appearance of a sarcostyle. That the dark and light bands

indicate different substances has been determined by the use of the polariscope, a microscope for the examination of materials by polarized

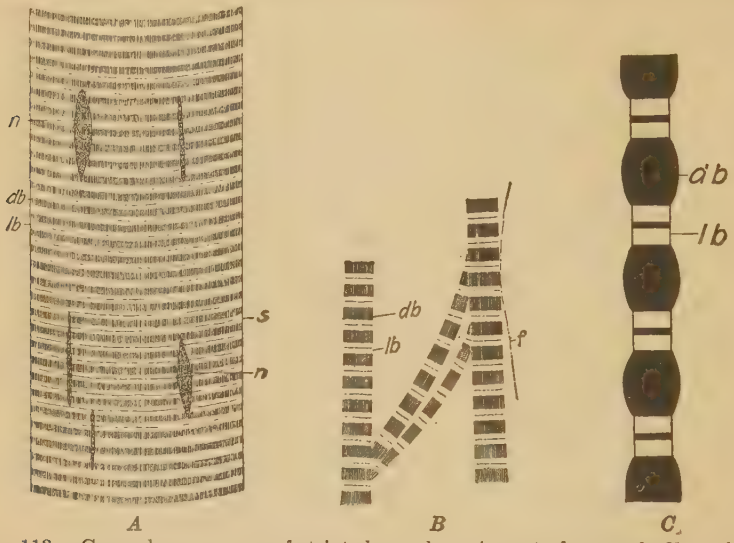

FIG. 113.—General appearance of striated muscle. *A*, part of a muscle fiber of a frog; *B*, part of a fiber teased out to show fibrillæ; *db*, dark bands; *lb*, light bands; *f*, fibrilla; *n*, nucleus; *s*, sarcolemma; *C*, a sarcostyle (fibrilla), diagrammatic; *db*, dark band; *lb*, light band with a thin band of dark material dividing it into two portions. (*A and B from Parker and Haswell's Textbook of Zoölogy.*)

light. When the fibrillæ are examined by polarized light it is found that the dark stripe of striated muscle is doubly refractive and the light stripe singly refractive. In fact, all contractile substance is doubly refractive. The significance of these optical properties is unknown.

Muscular Contraction.—Protoplasm is contractile, but vigorous contractions are possible only when the protoplasm has developed within it specialized contractile structures. These are of a fibrillar nature. In protozoa possessing structures capable of strong contraction these fibrils are known as *myonemes*.

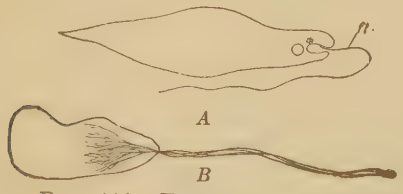

FIG. 114.—Euglena. *A*, individual showing flagellum (*fl*); *B*, fibrils in flagellum. (*A original; B after Dellinger in Journal of Morphology.*)

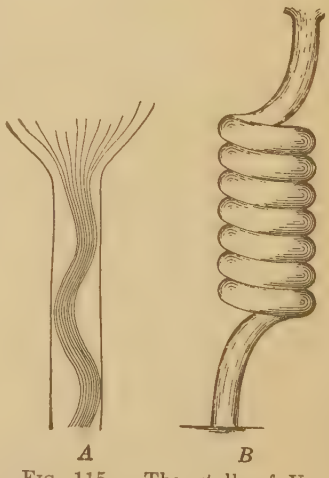

FIG. 115.—The stalk of Vorticella. *A*, arrangement of myonemes within the elastic sheath; *B*, stalk contracted.

Myonemes may be found in the flagellum of such animals as Euglena and Peranema and in the stalk of Vorticella. The flagellum of Euglena (Fig. 114) or Peranema is constructed of an external layer of elastic substance enclosing a number of myonemes which extend from the tip of the flagellum into the cytoplasm of the cell. The myonemes are twisted in the form of a loose spiral. Contraction of the myonemes or of certain of them bends the flagellum. The stalk of Vorticella is likewise composed of a sheath of elastic material enclosing a core made of myonemes (Fig. 115). Contraction of the myonemes causes the stalk to assume the form of a closely wound spiral. The spiral form is due to the fact that the myonemes occupy the form of a loose spiral in the sheath and perhaps to other peculiarities in the shape of the myonemes. Relaxation of the myonemes permits the elastic stalk to extend to its full length.

Chemical Changes during Muscular Contraction.—In higher animals, also, an attempt has been made to explain contraction by the activity of fibrils. The cells of smooth muscles contain myoneme-like threads, and striated muscles contain multitudes of sarcostyles. These have been supposed to cause the shortening of the cell, especially in striated muscle where the dark bands of the sarcostyles are swollen in contracted muscle. Most of the physiological explanations of the workings of these fibrils have had to be abandoned, however, and no satisfactory theory of muscular contraction exists at the present time. Certain chemical changes occur during muscular contraction, and inferences may be drawn concerning them. When a muscle contracts, lactic acid is formed, probably being released from some substance which contains the lactic acid group. Apparently the lactic acid is not a by-product but an essential part of the physico-chemical mechanism of muscular contraction and must be returned to its original condition in order that it may be again released for the next contraction. The lactic acid is put back as the result of an oxidation process in which oxygen is consumed and carbon dioxide liberated. The substance oxidized is doubtless a carbohydrate or a fat, since nitrogen metabolism has been shown not to be connected with muscular work. The carbohydrate is much more important in this oxidation process than the fat, although fats are capable of being used in the reaction. Muscular contraction results in the development of heat, partly from the tension of the fibrillæ and partly from the oxidation process. How these chemical changes might cause contraction is not clear. It has been suggested that the contraction of the cell is due, not to any action of the fibrils, but to a precipitation reaction of the sarcoplasm, as explained in Chap. III.

Locomotor System.—The structures upon which the muscles or other contractile elements act are very different and variously arranged in different animals. Locomotor organs or organelles of a simple type exist in most of the lower invertebrate animals but they can scarcely be

said to constitute a system. The simplest form of locomotor system consists of two sets of opposing muscles. It is essential to an understanding of the operation of any locomotor system in which muscle is involved to note that muscle is able to contract vigorously and thus exert considerable pull, but that its relaxation is passive, and its push negligible. A locomotor system depending on muscle as the motive power must therefore be composed of opposed muscles. In many of the worms, movement of the body is brought about by the alternate contraction of two main sets of muscles, the *longitudinal* and the *circular*. The longitudinal muscles run lengthwise of the body and the circular muscles encircle it. If the longitudinal muscles contract, the body is shortened, while if the circular muscles contract and the longitudinal muscles relax, the body is lengthened. Setæ or spines which increase the friction of the body on the surface over which the worm is creeping are present in many worms. In the leeches and in some other worms of parasitic habit, muscular sucking disks at the ends of the body, or at one end and at some other point on the ventral surface, enable the animal to adhere firmly in one region while the body is extended or drawn up. The alternate elongations and contractions of the body of these animals are accomplished, however, by the contractions of two sets of muscles in the manner described above.

Levers in Invertebrates.—In most animals employing muscles, a portion of the system consists of a set of levers moved by muscular contraction. Thus in each somite of the earthworm are four pairs of setæ whose outer ends project slightly from the body. These setæ are pivoted in the body wall and their inner ends are moved by the contractions of muscles (Fig. 116). The setæ play an important part in the locomotion of the earthworm because after the body is extended they catch on the soil and hold fast until the contraction of the longitudinal muscles shortens the body and brings up the rear. Since they are pivoted and are provided with muscles their angle with the surface can be changed. With the angle of the setæ changed the contraction and relaxation of the circular and longitudinal muscles move the worm in the opposite direction.

In the Arthropoda (including shrimps, crayfish, crabs, insects, and spiders) the locomotor organs likewise consist of sets of levers moved by the contraction of muscles regardless of whether the form of locomotion be swimming, creeping, walking, or flying. The hard parts are outside and the muscles inside, as shown in (Fig. 117, *A*). This relation of levers and muscles is reversed in the vertebrate leg (Fig 117, *B*), in which the bones are beneath the muscles. No detailed discussion of the musculature of any animal type can be given here.

Skeleton of Vertebrates.—The vertebrate skeleton largely determines the form of the body and serves as attachment for muscles and other tissues. It is composed of bones and cartilages united partly by

ligaments, is covered by the soft parts of the body, and is supplied with blood vessels and nerves. It may conveniently be divided into regions as indicated in Fig. 118. On more fundamental anatomical grounds it is also subdivided into the *axial* and the *appendicular* skeleton.

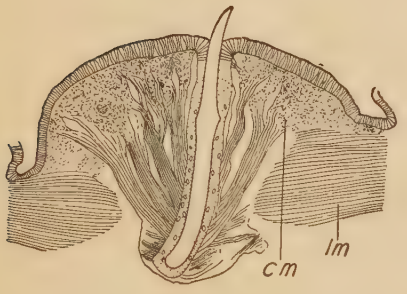

Fig. 116.

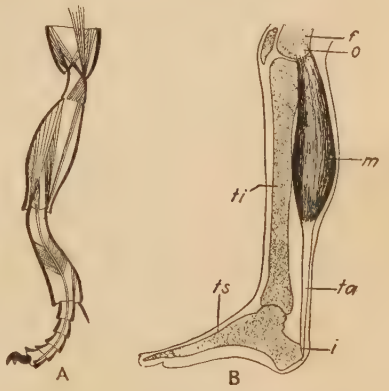

Fig. 117.

Fig. 116.—Seta and muscles in the earthworm, drawn from a longitudinal section anterior to the clitellum. *cm*, circular muscles; *lm*, longitudinal muscles. (*Original.*)

Fig. 117.—Relation of muscle to hard parts in appendages of insect and man. *A*, leg of insect; *B*, leg of man; *f*, femur; *fs*, skeleton of foot; *i*, insertion of muscle; *m*, muscle; *o*, origin of muscle; *ta*, tendo-Achilles; *ti*, tibia. (*A after Berlese; B after Hesse and Doflein.*)

Axial Skeleton.—The axial skeleton (Fig. 119) is made up of the *skull, hyoid apparatus, vertebral column, ribs,* and *sternum.* The skull furnishes a case for the brain, capsules for the organs of hearing and

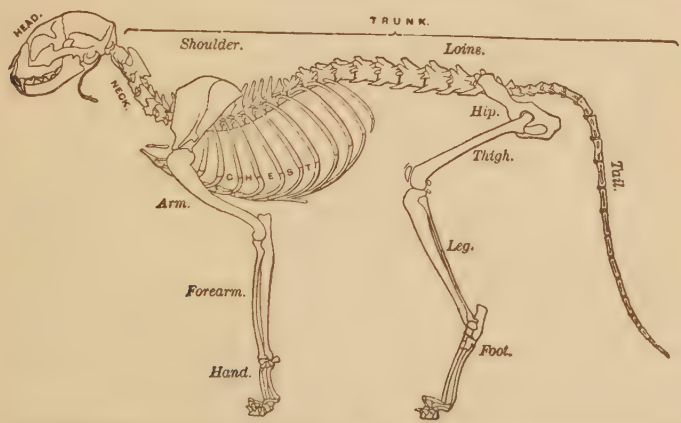

Fig. 118.—Regions of the vertebrate skeleton (cat). (*From Jayne's Mammalian Anatomy.*)

smell, and orbits for the eyes. It also includes the bones of the jaws. To it is attached the hyoid apparatus which is a bony or cartilaginous support for the base of the tongue.

The vertebral column is a jointed structure composed of a number (different in different species) of vertebræ placed end to end. Together they form a tube enclosing the spinal cord, and their outer surfaces form attachments for ligaments and muscles. The vertebral column is structurally differentiated into five regions, the *cervical*, *thoracic*, *lumbar*,

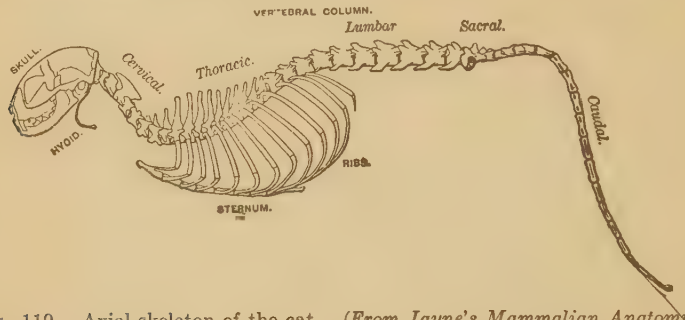

FIG. 119.—Axial skeleton of the cat. (*From Jayne's Mammalian Anatomy.*)

sacral, and *caudal* (see Fig. 119). The plan of a vertebra is shown in Fig. 120. It is composed of a heavy ventral portion, the *centrum*, from which arises a bony arch, the *neural arch*. The latter encloses the *neural canal* which is occupied by the spinal cord. From the sides of the arch two *transverse processes* project, and from the apex of the arch arises the

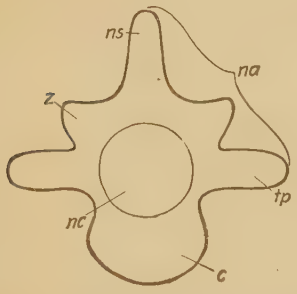

FIG. 120.—Diagram of a typical vertebra viewed from in front or from behind. *c*, centrum; *na*, neural arch; *nc*, neural canal; *ns*, neural spine; *tp*, transverse process; *z*, zygapophysis.

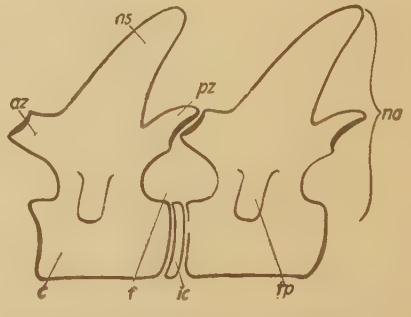

FIG. 121.—Diagram of two typical vertebræ viewed from the side, with anterior end at the left. *az*, anterior zygapophysis; *c*, centrum; *f*, intervertebral foramen through which nerves and bloodvessels pass; *ic*, intervertebral cartilage; *na*, neural arch; *ns*, neural spine; *pz*, posterior zygapophysis; *tp*, transverse process.

neural spine. One pair of articular processes or *zygapophyses* projects anteriorly and another posteriorly from the sides of the arch. The relations of the anterior and posterior zygapophyses and the articular faces of the centra of adjoining vertebræ are made clear in Fig. 121.

The forms of the vertebræ in different regions of the vertebral column are very different as shown in Fig. 119. In the thoracic region of an

animal having ribs the vertebræ have faces for the articulation of the ribs. In the sacral region the vertebræ in some animals are considerably thickened without great change in form, while in others they are much flattened and more or less fused into a plate-like structure, the *sacrum*. In the sacral vertebræ the neural canal is reduced in size and in the caudal vertebræ it is entirely absent.

Vertebræ articulate with each other chiefly by means of the centra. The articular surfaces of the centra may be concave or convex. Commonly one of the surfaces of a centrum is concave and the other convex, the convex surface of one vertebra fitting into the concavity of the next. But in some vertebræ both surfaces are concave and the space between the centra is filled with a lens-shaped pad of cartilage. Biconcave vertebræ are called *amphicœlous* (*amphi* = both and *koilos* = hollow). In the concavo-convex type of vertebra if the concavity is directed toward the head the vertebra is said to be *procœlous*, but *opisthocœlous* if the concavity is directed posteriorly. These types of vertebræ are illustrated in Fig. 122.

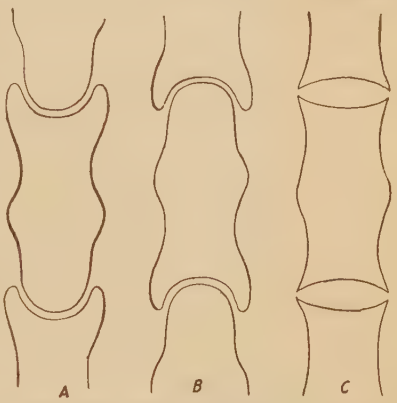

FIG. 122.—Three types of vertebræ. Only the centra and lateral processes are shown. Upper end is anterior. *A*, procœlous; *B*, opisthocœlous; *C*, amphicœlous.

Ribs are usually attached to the vertebræ in such a manner that they can be moved. Some of the hindermost ribs are free at their ventral ends while others are connected to the sternum or breast bone more or less directly by means of cartilage. The sternum is a bony or cartilaginous structure which lies in the median ventral part of the thorax. The number of pairs of ribs varies in different species.

Parts of Appendicular Skeleton.—The appendicular skeleton consists of the shoulder or *pectoral girdle* and the hip or *pelvic girdle* and the *fore* and *hind limbs*. The generalized plan of the girdles and limbs of animals higher than the fishes is shown diagrammatically in Fig. 123. In these appendicular skeletons each of the girdles is composed of three pairs of bones which are similarly arranged in the two girdles. Each side of the pectoral girdle is composed of a flat bone, the *scapula* or shoulder blade, directed dorsally, a *coracoid* bone connecting the scapula and the sternum (not shown in the diagram), and a *clavicle* which in some vertebrates also connects the scapula and the sternum. There may be a cartilage, the *precoracoid*, affixed to the posterior edge of the clavicle. A cavity, the *glenoid fossa*, located at the junction of scapula and coracoid, serves as the point of attachment of the fore limb. Each

side of the pelvic girdle consists of an *ilium*, *ischium*, and *pubis*. These three bones in a generalized skeleton are arranged similarly to the bones of the pectoral girdle. The cavity at the junction of the three bones is the *acetabulum*. In it is seated the head of the femur (thigh bone).

The bones of the arm and leg or fore and hind limbs are arranged according to the same plan and may be compared bone for bone, *humerus* with *femur*, *radius* and *ulna* with *tibia* and *fibula* respectively, *carpal* (wrist) bones with *tarsal* (ankle) bones, *metacarpals* with *metatarsals* (body of hand and foot respectively) and *phalanges* (bones of the digits)

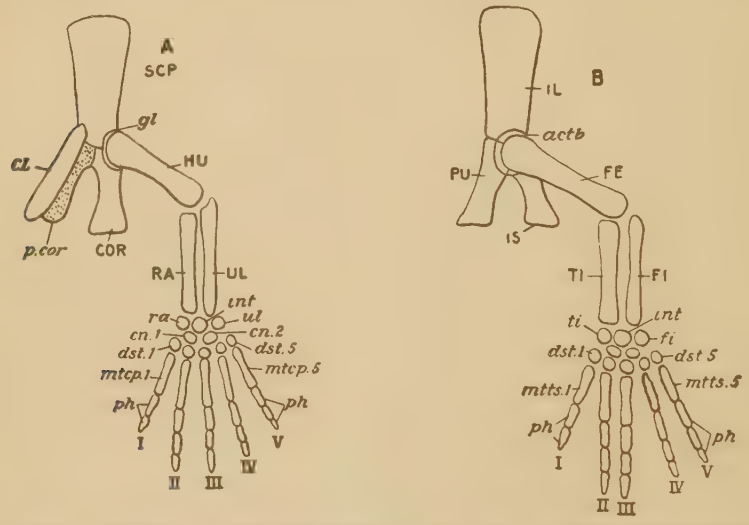

FIG. 123.—Diagrams of generalized fore (*A*) and hind (*B*) limbs with limb girdles. *actb*, acetabulum; *CL*, clavicle; *cn.* 1, *cn.* 2, centralia; *COR*, coracoid; *dst.* 1–5, distal row of carpals and tarsals; *FE*, femur; *FI*, fibula; *fi*, fibulare; *gl*, glenoid fossa; *I-V*, digits; *HU*, humerus; *IL*, ilium; *int*, intermedium; *IS*, ischium; *mtcp.*1–5, metacarpals; *mtts.* 1–5, metatarsals; *ph*, phalanges; *p.cor*, precoracoid; *PU*, pubis; *RA*, radius; *ra*, radiale; *SCP*, scapula; *TI*, tibia; *ti*, tibiale; *UL*, ulna; *ul*, ulnare. (*From Parker and Haswell's Textbook of Zoölogy.*)

of hand with those of the foot. Vertebrates with primitive limbs have five digits on fore and hind feet, but the limbs of specialized animals have undergone more or less extensive modifications from the original five-fingered and five-toed plan.

Nervous System.—The effective operation of the locomotor system, complicated as the foregoing pages show it to be, requires some means of coördinating its movements. Even fairly simple movements involve the simultaneous action of several muscles, while moderately complex movements may require participation of muscles all over the body. Smooth muscle constitutes an important part of several distinct systems of organs. To work effectively, these parts must work together, or in a

definite relation to each other. The necessary coördination is effected mostly by the nervous system, which also controls other activities, such as secretion.

The functions of the nervous system are various. It receives stimuli and transmits impulses, and serves as a regulating mechanism. These functions are accomplished through more or less specialized cells that may occur as scattered cells or grouped into nervous tissues. In most metazoan animals they are organized into nervous systems of varying degrees of concentration. Not present in the protozoa and sponges, nervous tissue is first found in the cœlenterates. In the hydroid polyps there is little specialized nervous tissue, but many ectodermal cells (Fig. 124) have elongated processes at their bases which serve the dual function

A *B*

FIG. 124.—Nervous mechanism of Hydra. *A*, neuromuscular cell from ectoderm; *B*, ectodermal nerve plexus. The long fibrils in the background are the contractile parts of neuromuscular cells. They lie in the mesoglœa. (*From Schneider.*)

of contraction and transmission of stimuli and are therefore properly called *neuromuscular* cells. Connected with these cells are sometimes other cells with long processes which serve as nerves for transmission of impulses.

Degrees of Centralization in Nervous Systems.—In jellyfishes, a ring of nervous tissue encircles the rim of the umbrella. Nerve cells of the ring are connected with a network of nerve cells in the umbrella, making a diffuse nervous system. This type of nervous system is the lowest in the animal scale. A more centralized nervous system is found in the flatworms and roundworms. In the flatworms, for example in the rhabdocœle and triclad Turbellaria, as shown in Figs. 125 and 126, there is a single *ganglion* or thickened mass of nervous tissue in the anterior end of the worm. From this ganglion two main nerve trunks extend to the posterior region of the body. Branches from the ganglion

and from the nerve trunks extend forward and to the lateral regions of the body. In the roundworms (Fig. 127) a ganglionic mass, the *nerve ring*, surrounds the esophagus and from this mass a dorsal and a ventral nerve trunk extend backwards. These are connected at intervals by *commissures*. From the nerve ring, branches extend forward and for a short distance backward.

In the Annelida (segmented worms) the nervous system is more highly developed but it is not highly centralized. It consists of a chain of ganglionic masses extending ventral to the alimentary tract from near the anterior end to the posterior end of the worm. In the anterior end the nerve cord divides, the two halves together encircling the pharynx

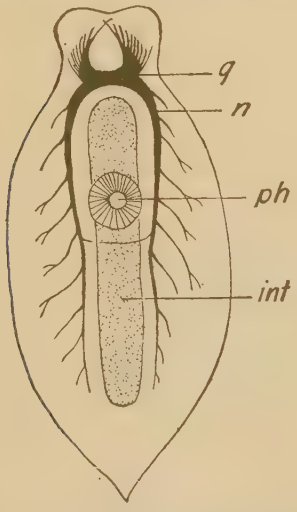

FIG. 125.—Digestive and nervous systems of a rhabdocœle turbellarian. *g*, ganglionic mass; *int*, intestine; *n*, nerve; *ph*, pharynx. (*After Lang.*)

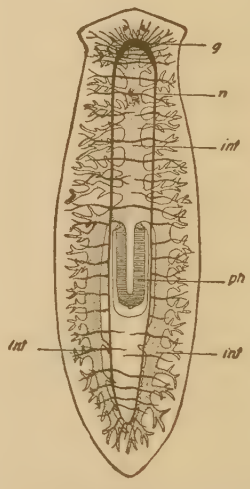

FIG. 126.—Digestive and nervous systems of a triclad turbellarian. *g*, ganglionic mass; *int*, intestine; *n*, nerve; *ph*, pharynx. (*After Lang.*)

and uniting above it, at the juncture of the pharynx and buccal pouch, to form the so-called *brain*, which in reality is no more than a pair of ganglia. From the brain, branches extend forward to the prostomium and to the other organs of the first few somites. There is a ganglionic mass in each somite, from which paired nerves extend out to the body wall and there branch out to all parts of the somite.

The nervous system of the Arthropoda has certain points in common with that of the Annelida. It lies ventral to the digestive system, which it encircles at the anterior end, and is composed of ganglia from which nerves arise. Whereas in the annelids the paired ganglia of each somite are fused into one ganglionic mass, in some Arthropoda they have a ladder-like arrangement as in Fig. 128, *A*, and in others the ganglia are fused into a chain (Fig. 128, *B*) like that seen in the earthworm. A

more advanced type of nervous system in which the ganglia of the chain are fused into larger ganglionic masses from which nerves arise may be seen in Fig. 128, *C*. In this type centralization has gone further than in the preceding forms.

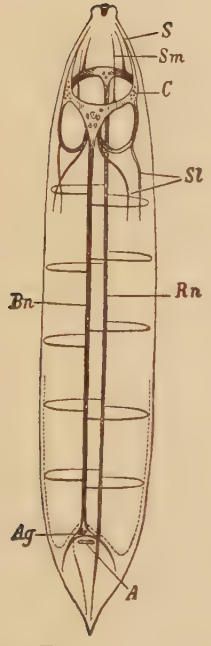

Fig. 127.

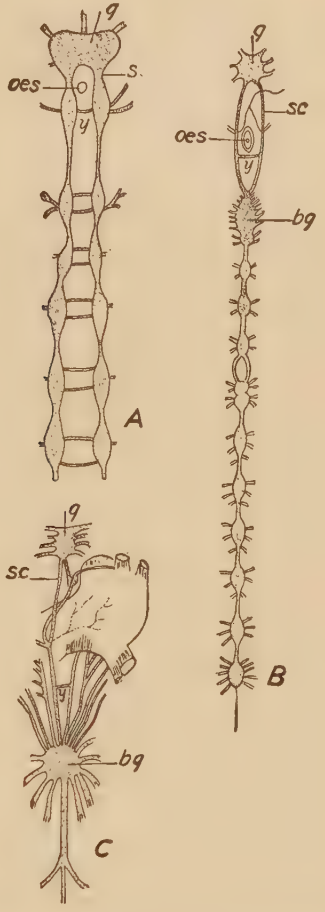

Fig. 128.

Fig. 127.—Nervous system of a roundworm, diagrammatically represented. *A*, anus; *Ag*, anal ganglion; *Bn*, ventral nerve; *C*, lateral ganglion of nerve ring; *Rn*, dorsal nerve; *S*, anterior lateral nerve; *Sl*, sublateral nerve; *Sm*, submedian nerve. (*From Sedgwick's Student's Textbook of Zoölogy, after Butschli.*)

Fig. 128.—Nervous systems of arthropods, showing advance in centralization. *A*, ladder-like nervous system of *Limnadia*, anterior portion only (*after Klunzinger*); *B*, *Astacus fluviatilis* (*after Vogt and Yung*); *C*, *Maia squinado* (*after Milne-Edwards*); *bg*, subesophageal ganglion; *g*, brain or supraesophageal ganglion; *oes*, esophagus; *sc*, esophageal commissure; *y*, postesophageal commissure. (*From Sedgwick's Student's Textbook of Zoölogy, after Lang.*)

Concentrated System of Vertebrates.—Concentration of the main masses of the nervous system into organs of limited extent is carried farther in the Vertebrata where the nervous system is highly organized.

Even within the group of the Vertebrata, the nervous system shows a considerable increase in complexity and in the degree of centrali-

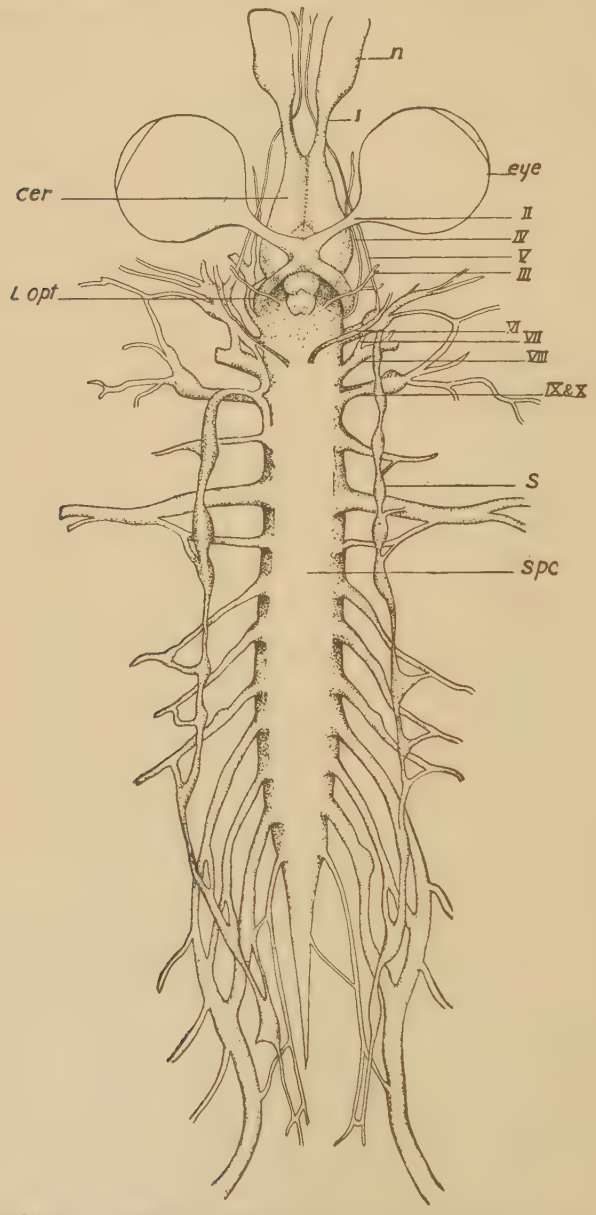

FIG. 129.—Nervous system of the frog, showing cranial and spinal nerves and sympathetic system, ventral view. *I*–*X*, cranial nerves; *cer*, cerebrum; *L opt*, optic lobe; *n*, nasal sac; *s*, sympathetic system; *spc*, spinal cord. (*After Wiedersheim.*)

zation from the condition in the lower vertebrates to that in man. The central nervous system of the frog (Fig. 129) consists of a moder-

ately large mass of nervous tissue, the brain, located in the head, and a spinal cord, dorsal to the alimentary tract, extending backward from the brain almost to the end of the trunk. From the brain arise 12 pairs (10 in lower vertebrates) of cranial nerves which extend to and innervate the organs of the head and neck and many organs of the trunk. The distribution of these nerves is practically the same in all the craniate vertebrates (those possessing crania or skulls). From the spinal cord paired nerves originate, corresponding to the somites of the body as indicated by the vertebræ. Each spinal nerve originates by two roots, dorsal and ventral (Fig. 132). The dorsal root just median to its union with the ventral root expands into a ganglion which is composed of nerve cells whose processes make up much of the nerve. Originating in the brain (Fig. 129) and extending down on either side of the spinal cord are two strands of nervous tissue which are connected by nerves with the dorsal root ganglia. These strands with their branches and ganglia, which may be widely separated from the strands, comprise the *sympathetic nervous system.*

Position of the Nervous System.—In comparing the central nervous systems of the invertebrates and vertebrates, emphasis has been placed chiefly on the greater degree of concentration of this system in the vertebrates. Another morphological difference having a probable evolutionary significance is in the location of the nerve cord, which is dorsal to the digestive canal in all vertebrates, and ventral to it in the higher invertebrates. In both groups the anterior ganglionic mass or brain lies anterior or dorsal to the mouth. In the higher invertebrates the nerve cord is connected with the anterior ganglionic mass by a pair of commissures which encircle the digestive tract.

Nervous Control.—There are three means of controlling the mass of cells of which a metazoön is composed. These are (1) the tissues which bind the organs together and the skin which encloses the whole, (2) hormones and other substances which act by the virtue of their chemical nature, and (3) the nervous system. Although the first of these modes is largely mechanical, it is of some importance, for without the mechanical effect of the connective and muscular tissues there could be no unification of the various parts into an individual. The second method of unification and control (by means of hormones or other chemical substances) has already been illustrated in an earlier chapter. It is exemplified by the discharge of pancreatic secretions in response to stimulation of the pancreas by secretin. This mode of control is automatic, that is, the various events or circumstances leading to the end result stand in the mutual relation of links in a chain. Control by hormones is involuntary, not under control of the will. By this chemical means of regulation many of the metabolic activities of the body are wholly or partly directed. The nervous system plays a rôle in certain instances of

hormone control; but this system also directs a large number of activities with which the organs of internal secretion and their products have nothing to do. The nervous system not only coördinates the activities of many of the internal organs but also controls the reactions of the individual to conditions of the environment. Much of this control is performed without thought on the part of the individual.

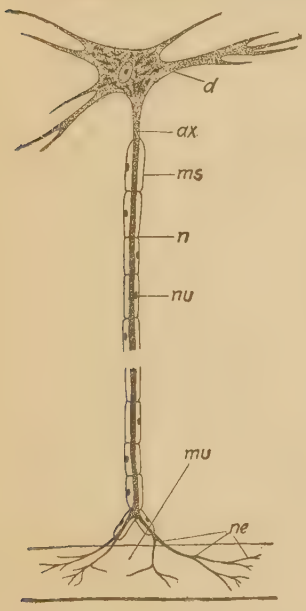

FIG. 130.—Diagram of a typical neuron. *ax*, axon; *d*, dendrite; *ms*, medullary sheath; *mu*, muscle; *n*, node; *ne*, nerve endings; *nu*, nucleus of cell of medullary sheath.

Unit of Structure of Nervous System.—The unit of structure of the nervous system is the *neuron*. The neuron is a cell possessing a number of fine projections which sometimes extend to great lengths. These projections are of two kinds, distinguished from one another, not by structure, but by their normal functioning. Those which normally conduct impulses toward the body of the neuron are called *dendrites;* those which convey impulses from the body of the neuron are *axons*. Which direction the impulse travels, and hence which processes are dendrites or axons, is determined by the manner in which the given neuron is connected with other neurons. Figure 130 diagrammatically represents the parts of a typical neuron, and three kinds of neurons are shown in Fig. 131.

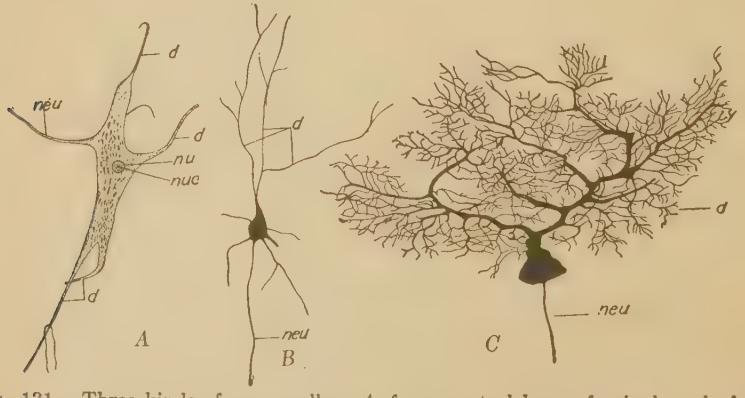

FIG. 131.—Three kinds of nerve cells. *A*, from ventral horn of spinal cord of an ox; *B*, from cortex of cerebrum of a cat; *C*, Purkinje cell from cerebellum of a cat; *d*, dendrite; *neu*, axon; *nu*, nucleus; *nuc*, nucleolus. (*B and C from Golgi preparations. Original.*)

These cells, which are strictly speaking the only constituents of the nervous system, are bound together by connective tissue, and the masses thus formed are supplied with blood vessels.

The functions of the nervous system depend largely upon the manner in which the neurons are connected into neuronic systems and upon the character and positions of the terminations of the axons and dendrites. These systems are of varying degrees of complexity.

The Reflex Arc.—A simple reflex arc is composed of one *sensory* neuron and one *motor* (activator) neuron. Such an arc is diagrammatically represented in Fig. 132. The example chosen involves the spinal cord and a spinal nerve. The dendrites of the sensory neuron branch out between the cells of the skin. The body of the neuron lies in a ganglion, and its axon passes into the dorsal horn of the gray matter of the spinal cord where its terminal branches come in contact with the dendrites of the motor neuron. The body of the motor neuron lies in the ventral horn of the gray matter and its axon emerges from the ventral

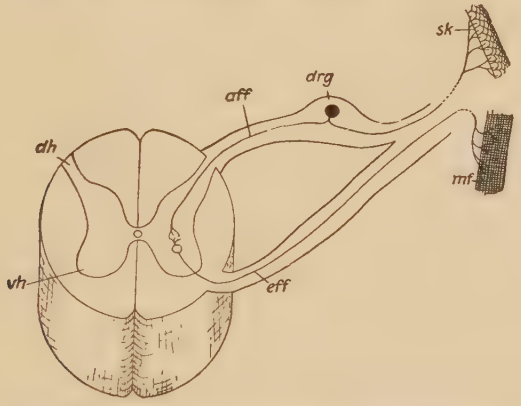

FIG. 132.—Diagram of a simple reflex arc involving the spinal cord. *aff*, afferent fiber; *dh*, dorsal horn of spinal cord; *drg*, dorsal root ganglion; *eff*, efferent fiber; *sk*, skin; *mf*, muscle fiber; *vh*, ventral horn of spinal cord.

side of the cord, passes by the ganglion, and then runs for some distance in the same bundle (nerve) with the dendrite of the sensory neuron. The axon of the motor neuron terminates in a muscle in the example chosen. In other similar reflex arcs it may end in a gland. Stimulation of the sensory endings in the skin causes an impulse to pass along the dendrite and axon of the sensory neuron to the motor cell and thence out to the muscle which is stimulated to contract. If the axon of the motor or activator neuron ends in a gland, stimulation of the sensory endings causes discharge of the glandular secretions. An action caused by an impulse carried over a reflex arc is known as a *reflex action.*

It seems to be well established that there is no organic union between the axon of the sensory neuron and the dendrites or body of the motor neuron, for these parts are simply in contact. The point of contact is called the *synapse.* The synapse has been likened to a valve in a water pipe, which is so constructed as to permit flow in one direction only.

If in the reflex arc an electrical or other stimulus be given to the motor neuron, the impulse may pass along the motor neuron in both directions, but that part of the impulse which travels backward, that is, in the direction opposite to that in which impulses normally move, can only go to the synapse; it is unable to pass over to the sensory neuron.

Few reflex arcs are as simple as indicated in the diagram. More complicated reflex arcs may involve one or more neurons intercalated between the sensory and the motor neuron. In these more complicated reflex arcs the axon of the motor neuron may emerge from the spinal cord at a point either above or below (that is, nearer to or farther from the brain than) the ganglion containing the body of the sensory neuron. The sensory neuron may also be brought into contact with dendrites of cells whose axons ascend the cord and are connected with centers in the brain. Thus it is possible that a stimulus applied to the skin may yield a reflex action and also appeal to the consciousness of the subject. An example of such a reflex is the recoil upon touching a hot object. The act is performed without volition but the subject is conscious of the stimulus and the response.

Reflex Actions.—Reflex actions may involve motion, as in shivering, a response to the stimulus of cold, the roughening of the skin so that it presents the appearance known as goose flesh, the enlargement or contraction of the pupil of the eye with changes of light intensity, and withdrawal of the hand from any source of sudden pain. Other reflexes are the activation or inhibition of glandular secretion. An example is the flow of saliva upon irritation of the mouth or throat. The emotions of anger and fear inhibit reflexly the discharge of many secretions of the digestive glands. Some actions which normally are reflexly controlled may also be voluntarily controlled, and many complex actions which at their inception were voluntary eventually come to be automatic. Examples of such automatic processes are walking, running, dancing, skipping the rope, swimming, writing, and running scales at the piano. Here also may be included the complicated movements of muscles of the mouth and vocal organs during speech. Each of these processes is due to a large number of reflex actions, occurring in part simultaneously, in part consecutively, but all related to one another. The reflex mechanism is sufficiently complicated to care for two or more complex series of reflex actions at the same time. For instance, one may swim and talk, or play the piano and sing. In some of these instances part of the action may be voluntary, the remainder involuntary.

Functions of the Spinal Cord.—The spinal cord acts as a system of reflex centers which control the activities of various glands, visceral organs, and skeletal muscles. In addition to this function it serves as a pathway to and from the brain. In man, more than half a million neurons enter the cord through the dorsal roots of the spinal nerves. These

bring in afferent impulses from the peripheral endings of sensory cells. By means of neurons which lie in the white portion of the cord and which end in the brain, impulses may be carried upward to the brain while a multitude of other neurons which originate in the brain form the pathway of impulses from the brain to the ventral roots of the spinal nerves. In terms of a telephone system the spinal cord may be likened to a series of centrals for the handling of local messages and to a great trunk line which transmits long distance messages arising at any point on the periphery of the system or at the great central station, the brain. Unlike the telephone system, however, messages (impulses) can pass only in a certain direction on the line (neurons). Hence in every reflex arc there is a neuron for carrying in the impulse initiated by the stimulus and another neuron for carrying out the impulse from the controlling center to the organ which executes the appropriate action.

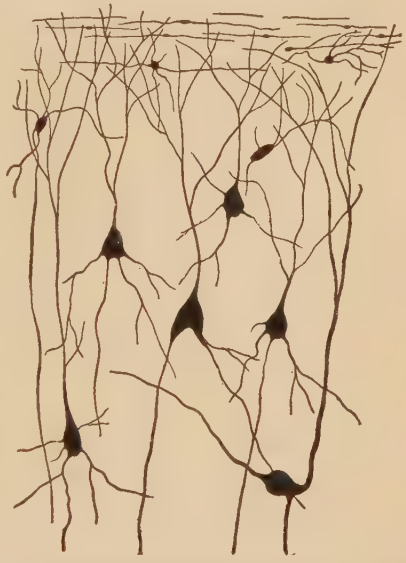

FIG. 133.—Cells of the cortex of the cerebrum of a cat as shown in a Golgi preparation.

Functions of Divisions of Brain. The chief divisions of the brain are the *cerebrum*, *cerebellum*, and *medulla oblongata*. The cortex of the cerebrum, that is, the layer of gray substance which covers the organ and dips down into the furrows, is the seat of intelligence and of conscious sensations. It is the organ of memory associations. In higher animals it controls voluntary motions. In the cerebrum the neurons of one side (right, for instance) give rise to axons which cross to the other side (left) as they extend down to lower centers, and there terminate around cells whose axons in turn go to the muscles (left). Hence the movements of the muscles of one side of the body are controlled by neurons located in the opposite side of the cerebrum. This statement is not entirely true since certain muscles are connected to neurons in both sides of the brain. The cells of the cortex are mostly of the type illustrated in Fig. 133.

There still exists much difference of opinion regarding the function of the cerebellum. In some manner it regulates the mechanism of automatic movements. It has the effect of coördinating voluntary movements, especially the complex movements of equilibrium and locomotion. It is not believed that the cerebellum is responsible for a high degree of consciousness, if any. Unlike the relations of the cerebrum to muscles,

each half of the cerebellum is connected with the organs on the same side of the body with itself. The cells of the cerebellum are of several types and the arrangement of fibers is very complex.

The medulla oblongata includes centers which control the activity of the organs of circulation and respiration. Through the vagus (tenth cranial) nerve it has an inhibitory effect on the heart. It also controls the movements and secretions of the alimentary canal.

The Nerves.—The twelve pairs of cranial nerves (those that emerge from the central nervous system within the skull) include the nerves of special sense and others that are distributed to the face, throat and trunk. Some of them are sensory, others motor. The spinal nerves, as explained above, arise from the spinal cord by two roots, of which the dorsal contains sensory neurons, the ventral one motor neurons. The sympathetic nervous system supplies the smooth muscle of the viscera

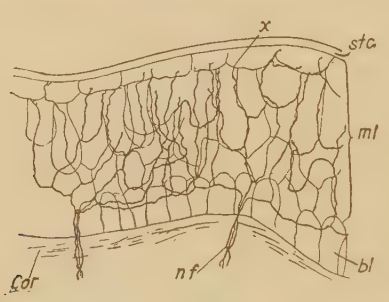

FIG. 134.—Termination of afferent fibers in the skin of the salamander, *Salamandra maculosa*. *bl*, basal layer of skin; *cor*, corium; *ml*, middle layer; *nf*, nerve fibers; *stc*, stratum corneum; *x*, end of a terminal. (*From Schneider after Retzius.*)

cardiac muscles, blood vessels, glands, and erector muscles of the hair. Impulses carried by this system originate in the central nervous system in centers lower than the cerebral cortex. These impulses are involuntary.

Sensory Nerve Endings.—The dendrites of the afferent neurons originate in the skin and in the tissues of the body, especially in epithelium, muscle and connective tissues, and in organs of special sense. Each neuron when stimulated at its peripheral ending conveys an impulse to the central nervous system where it usually gives rise to an impulse that finds expression in the contraction of muscle or discharge of a glandular secretion. Besides initiating this reflex action the stimulus may cause an impulse to be carried over an appropriate path to a higher nervous center, where it enters the consciousness of the subject, producing a sensation of some sort. The particular kind of sensation aroused by the stimulation depends not so much upon the character of the stimulus as it does upon the kind of sense organ involved and the nature of the central connections. The classes of sensations which originate from stimulation of body surfaces and tissues other than the organs of special sense are those of

pressure, warmth, cold, pain, strain sensation from muscle and tendon, and various organic sensations. For the mediation of each of these sensations there must be appropriate sensory endings and nerve cells. The types of endings responsible for the mediation of the different classes of sensations cannot be distinguished on the grounds of histological structure but only by experiment. Figure 134 illustrates the termination of an afferent fiber in the skin of the salamander.

Organs of Special Sense.—The sensations of light, sound, taste and smell are not perceived through scattered sensory cells but through the grouped sensory cells of the organs of special sense, the eyes, ears, taste buds and olfactory epithelium respectively. Although the structure of these organs is very different the sensitive cells of each may be considered to be modified ectodermal epithelial cells connected in some manner with the central nervous system. The sensory cells of the ear and of the retina of the eye and of the taste buds are connected with the central nervous system by means of nerve cells whose peripheral branches are in contact with the bodies of the sensory cells and whose inner branches terminate in the central nervous system. The cells of the olfactory epithelium, on the contrary, have no intercommunicating cells between them and the central nervous system but each cell has a fine process which extends from the base of the cell to the central nervous system.

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CHAPTER IX

REPRODUCTION

Even the earliest observers of nature, crude though their ideas of life were, can hardly have escaped the knowledge that new individuals are brought into existence by other individuals of the same kind. Animals have been domesticated from time immemorial, and the method of producing new individuals among such animals must have been well known. Nevertheless early writings reveal a common belief that many animals even among the higher groups arose occasionally in some other manner. Moreover, there was a host of animals of simpler structure and unknown habits which were supposed regularly to come into existence without the intervention of other living beings. This conception of the origin of individuals is comprised under the term *abiogenesis* or *spontaneous generation*.

FIG. 135.—A barnacle, *Lepas anatifera*, once thought to arise by spontaneous generation.

FIG. 136.—Francesco Redi, 1626–1697. (*From Garrison's History of Medicine, W. B. Saunders Co.*)

Spontaneous Generation.—For centuries before the invention of the microscope it was commonly believed that living things arose spontaneously from non-living material or that more complex animals might arise in very short time from simple animals or from the dead bodies of animals or plants. The ancient Greeks believed that animals arose from mud at the bottom of bodies of water. Similar ideas have been current among the people of many nations. Directions may be found in certain old books for the artificial generation of bees, and even of mice.

During the middle ages strange ideas were held as to the transmutation of animate objects into complex animals. The barnacle *Lepas anatifera* (Fig. 135) was then considered to be the fruit or leaf of a tree, probably because it was found attached to the branches of floating trees or driftwood thrown upon the beach by storms. From these barnacles in turn geese were supposed to originate.

Many erroneous ideas thus arose and were accepted largely because they were proposed by men of some authority, and in part because there were few men fitted by reason of their learning and temperament to observe carefully and to plan and execute critical experiments by which these ideas might be tested. Authority ruled. Eventually, however, there arose among men a spirit of inquiry which impelled them to question authority and to demand verification by means of observation and experiment. One skeptical inquirer was Redi (Fig. 136), of Italy.

Experiments Discrediting Spontaneous Generation.—Before Redi's time people accepted apparently without question the idea that maggots were generated spontaneously in meat. Redi, as a result of his observations on the actions of flies about meat, conceived the idea that there might be some connection between the flies and the maggots. To test the new idea he devised some experiments. He put some meat into a jar and covered it with parchment. The meat putrefied but there were no maggots. When he substituted a fine gauze cover for the parchment the flies perceived the odor of meat about the dish, but since they could not reach the meat they laid their eggs on the gauze where the eggs hatched. By a series of experiments of this sort Redi showed how organisms might arise in a variety of situations without appealing to the idea of spontaneous generation.

By the introduction, early in the seventeenth century, of the microscope as a means of study opportunity was given to investigate a whole new world of living things whose existence could only have been suspected. Leeuwenhoek (Fig. 6) discovered bacteria and protozoa about 1683. Many investigators believed that these minute things were the beginnings of more complex organisms which were in process of originating *de novo*. These ideas were retained with considerable tenacity for a hundred years or more, until experiments were performed which rendered them untenable.

Spallanzani, 1777, objected to the methods employed in making the cultures of microörganisms used in support of the theory of spontaneous generation. He filled flasks with culture solutions in which bacteria and other low organisms were supposed to originate, boiled the contents and hermetically sealed the flasks. These flasks were then subjected to conditions thought to be favorable to the formation of new living things, but no organisms appeared. When, in response to criticisms of his method, Spallanzani tapped the glass making a slight fracture in

order to let in the air, organisms always appeared. No more critical experiments seem to have been performed until about 1836 when Schultze perfected a method for admitting air to the culture medium. He drew the air through a series of tubes containing acids or strong alkalies which he believed would kill any organisms in the air. Schwann in 1837 and others used still other methods of removing possible organisms from the air before allowing it to come in contact with the culture medium. Cotton wool was used by some to plug up the containers. Pasteur (Fig. 137) in 1861 devised a flask (Fig. 138) with a tube fused in the side. The tube was so bent (down, then up, then down) that no particle of dust could pass the curve in which a droplet of water was left by condensation after boiling. When the flask had been partly filled with putrescible material and then sterilized its contents remained without putrefaction. Pasteur's experiments were so care-

Fig. 137.

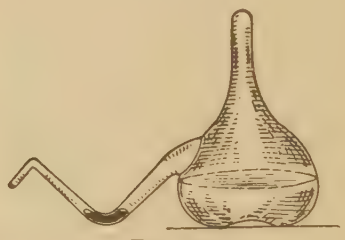

Fig. 138.

Fig. 137.—Louis Pasteur, 1822–1895. (*From Garrison's History of Medicine, W. B. Saunders Co.*)

Fig. 138.—Flask used by Pasteur in experiments upon spontaneous generation. The open top was sealed after the flask was filled with a nutrient solution. After boiling, water vapor condensed and filled the low curve in the side tube thus preventing access of organisms borne by the air. (*After MacFarland.*)

fully carried on and were so extensive that the idea of spontaneous generation in its old form was generally abandoned. Careful experiments by the physicist Tyndall and the work of Lord Lister who made application of the results of Pasteur to surgery did much by confirming Pasteur's teachings to overthrow the idea of spontaneous generation.

Pasteur's investigations and teaching resulted in the origin of a whole new field of biological investigation, namely, bacteriology. The investigations of the bacteriologists show beyond a doubt that bacteria are not now originating *de novo* in cultures. Bacteria originate only from preexisting bacteria. If a bacteriologist finds in a culture a bacterium which he did not put there he ascribes its presence to contamination through air currents or instruments, or to faulty sterilization. The old idea of

spontaneous generation is now recognized as untenable, and present-day organisms are known to arise only from previously existing organisms through some form of reproduction.

Modern Idea of Spontaneous Generation.—Many biologists believe that while living things are not originating under present conditions, life at some time in the past originated by a combination of the proper elements when conditions were other than at present. This belief is sometimes designated the modern theory of spontaneous generation. Some investigators still hope that a simple living substance may be synthesized under special conditions of temperature, moisture, and pressure by the combination of the elements carbon, nitrogen, oxygen, hydrogen, phosphorus, iron, etc., usually found in protoplasm. This hope, which has not been widely entertained, has so far been disappointed, and, although chemists have been able to synthesize many organic compounds once thought to be incapable of production by other means than the activities of cells, the manufacture of the complex mixture called protoplasm is still beyond their reach.

The modern conception of spontaneous generation differs from the ancient view in that it does not propose to account for the origin of organisms of the kind we now know. It therefore has no relation to ideas regarding reproduction, and further discussion of it is omitted.

Reproduction.—Since no living thing can maintain itself for an unlimited period of time the ability of the members of a species to produce others individuals is most important from the standpoint of the welfare of the species. Living organisms provide for increase of numbers of individuals by a variety of reproductive methods which fall into two general categories, namely, *sexual* and *asexual* reproduction. Sexual reproduction as a rule involves two parents, and the union of two germ cells or their equivalents. Asexual or non-sexual reproduction includes all forms of reproduction not involving germ cells or their equivalents.

Sexual Reproduction.—Sexual reproduction is a well-nigh universal method of reproduction. It is employed by representatives of every phylum of animals and by many of them to the exclusion of the asexual method. It is also used by the plants, except the bacteria. A phenomenon of such widespread (almost universal) occurrence must have considerable import.

In general terms the basis of sexual reproduction is the union of two cells to form a single cell, the *zygote*, which by its subsequent divisions produces a new individual if the uniting cells are of metazoan origin, or a new series of individuals if they are of protozoan origin. Not all cells are capable of uniting in this way, and cells which are capable of this act are called *gametes*. Certain gametes are relatively large, contain a considerable amount of nutritive material, and are non-motile; these are called *ova* (singular, *ovum*), or *eggs*. Other gametes are minute,

often a very small fraction of the size of the ova of the same species. These are poorly supplied with nutritive material, have little cytoplasm, and usually are motile; they are known as *spermatozoa* (singular, *spermatozoön*). The individuals in which eggs develop are females, and those in which spermatozoa develop are males.

Sexual Reproduction in Metazoa.—In metazoa the germ cells, ova and spermatozoa, are the direct descendants of the primordial (first) germ cells. They retain their power of uniting to initiate the development of a new metazoan individual. All other cells have completely lost this power. In a sense the germ cells are primitive cells, resembling the protozoa in respect to their potentialities. They are stored in the metazoan body where they live at the expense of the somatic cells but without taking active part in the general body functions. As the time for sexual reproduction draws near the germ cells undergo a certain process of development or of preparation for the sexual act. This preparatory pro-

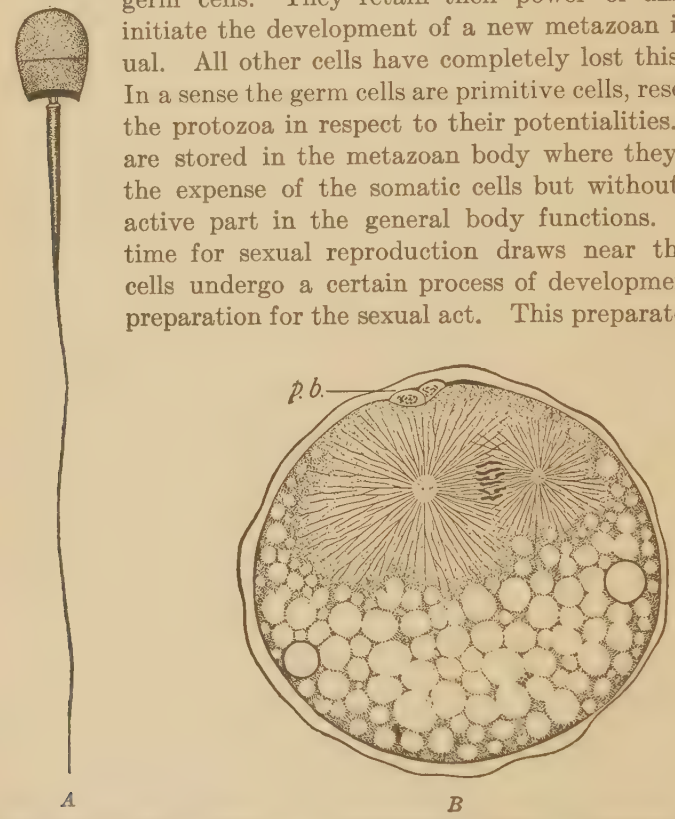

Fig. 139.—Sperm cell and ovum. *A*, spermatozoön of badger; *B*, fertilized ovum of Nereis with two polar bodies, *pb*. (*A from Dahlgren and Kepner's Principles of Animal Histology; B from Wilson's The Cell. Courtesy of The Macmillan Company.*)

cess, known as *maturation*, is discussed in detail in Chap. XI but its essentials may be stated here. Maturation of the ovum consists in the main of two mitoses by which three or four cells are produced. Of these cells one is much larger than the others and its nucleus has one-half the usual number of chromosomes. The small cells are called *polar bodies* and are non-functional. Maturation of the sperm cell does not differ essentially from maturation of the ovum, except that the process results regularly in the formation of four relatively small cells

of about equal size, all of which are usually functional. Like the eggs they have half the usual number of chromosomes. The male germ cells must then be transformed, by a striking change of shape, into spermatozoa. A sperm cell and an ovum with polar bodies are illustrated in Fig. 139.

When matured spermatozoa and eggs of the same or closely related species are brought together, the actively motile spermatozoa meet and penetrate the eggs. Usually but one sperm cell can enter an egg. After its entrance other spermatozoa are excluded, either by a change in the surface of the egg or by some other mechanism. The spermatozoan nucleus and egg nucleus arrange themselves side by side; their chromatin undergoes changes in arrangement, assuming the form of a thread and then of chromosomes; a spindle is formed and the zygote divides by mitosis. This sequence of events indicates that the egg is induced to divide because of some stimulus given to it by the spermatozoön.

Sexual Reproduction in Protozoa.—In Amœba and other protozoa having pseudopodia, so far as sexual reproduction is known, union between *similar* individuals is the rule. In many of the species where it has been observed it apparently occurs only at rare intervals.

The flagellate protozoa and the protozoa reproducing by spores produce gametes which may be of the same size or of different sizes. If the gametes are of the same size they are said to be *isogametes*. In this case, however, the gametes are perhaps alike only in size, since it is conceivable that there are internal differences which are not visible. The gametes may both be motile or the smaller only may be motile. In *Heteromita lens* (Fig. 140) and in some other species the isogametes are of the same size as the vegetative cells. In *Pandorina morum* (Fig. 141) the gametes are of two sizes, and two combinations are possible: two small gametes, or one small and one large, may fuse, but not two large ones.

Eudorina elegans (Fig. 142) shows well-marked differentiation into large and small gametes and union always takes place between a large and a small gamete. Union of unlike gametes is known as *anisogamy* in contrast to *isogamy* (union of like gametes). The large gamete of Eudorina is not only large but is well supplied with nutritive material. It is unlike the ovum of the metazoa in that it is motile. The small gamete has little stored nutritive material and has motor organs. Pleodorina and Volvox have similar reproductive methods; but the macrogamete of Volvox or of *Pleodorina californica* may be properly called an ovum, since the cell has no motor organs (at least in its later stages), and something comparable to maturation appears to occur. The small gametes of Eudorina, Pleodorina, and Volvox are similar in their general features.

In the examples of protozoan sexual reproduction cited, there is complete fusion of one gamete with the other, whether the union is between

like or unlike gametes; but in some ciliated protozoan species which possess a macro- and a micronucleus, the gametes do not fuse. There is in such cases merely an exchange of portions of the micronuclei and perhaps

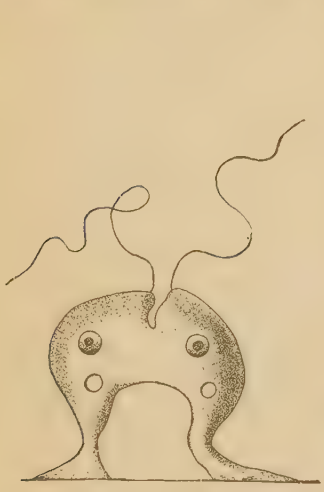

Fig. 140.

Fig. 141.

Fig. 140.—Isogamy in *Heteromita lens*. (*After Kent.*)

Fig. 141.—Reproduction in *Pandorina morum* Borg. *A*, normal colony; *B*, daughter colonies arising by division of mother cells within old colony, ×475; *C–H*, gametes (*g*), formation of zygospore (*z*) and its development. (*From West after Pringsheim.*)

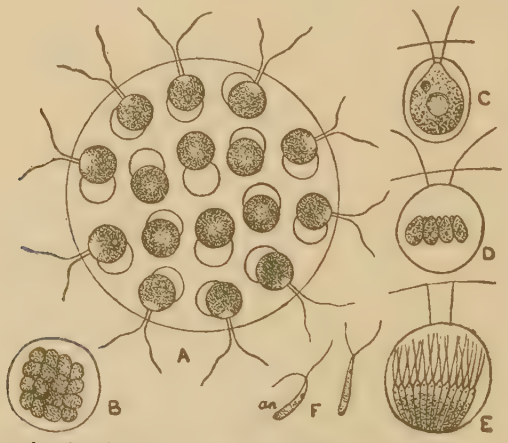

Fig. 142.—Reproduction in *Eudorina elegans* Ehrenberg. *A*, adult colony ×475; *B*, daughter colony produced by division of one of the cells of such a colony as in *A*, ×730; *C–E*, development of spermatozoa from a mother cell; *F*, spermatozoa. (*From West after Goebel.*)

of some cytoplasm. This union for the exchange of nuclei is called *conjugation*. The *complete* fusion of protozoan cells has sometimes been given another name (copulation) which, however, is used in a totally

different sense with respect to the metazoa, so that it seems wise here to refer to such complete unions simply as fusion. The process of conjugation is here described and illustrated as it occurs in Paramecium.

At the time of conjugation (Fig. 143, *A*) two individuals of Paramecium come together with their oral surfaces in contact. They are

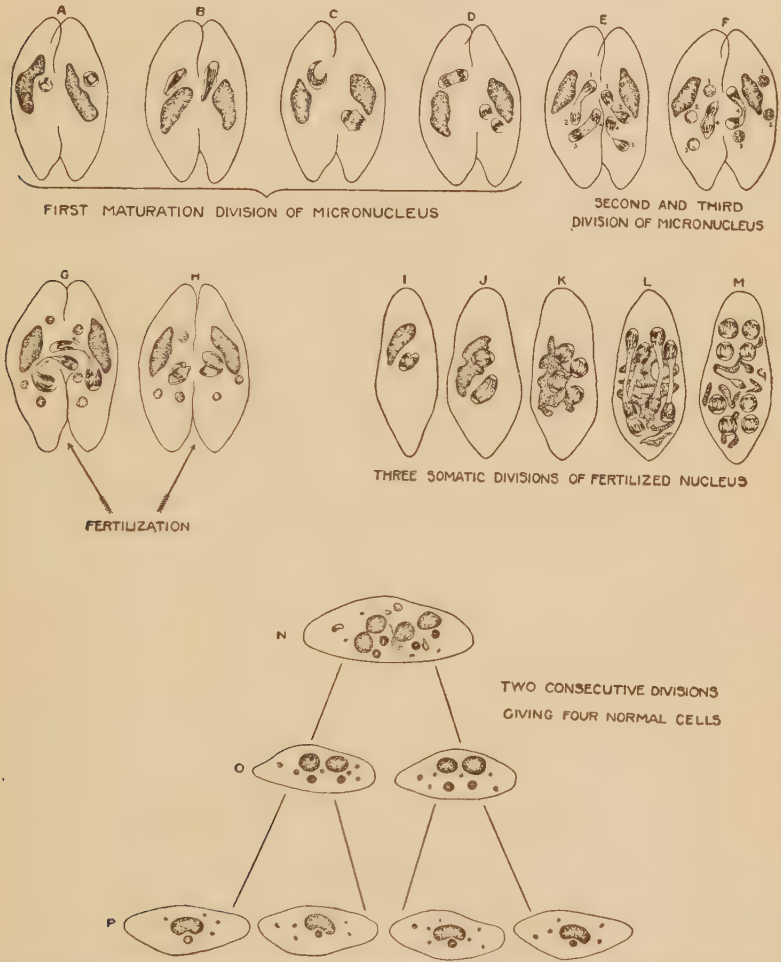

FIG. 143.—Diagram of the process of conjugation in Paramecium. The reference to maturation in the figure will be clear only after a perusal of Chap. XI. (*From Calkins, Biology of the Protozoa.*)

held in this position for a time because of the stickiness of the protoplasm on those surfaces. While they continue to swim about internal changes in the micronucleus and macronucleus of each individual take place. The micronucleus of each Paramecium divides by a process of modified or primitive mitosis (*B*, *C*, *D*), and then each half divides again. Thus

each micronucleus gives rise to four micronuclei (Fig. 143, *E*). Of these micronuclei, three undergo degeneration, and the one remaining in each Paramecium divides again into two parts, usually of unequal size (*F*). The smaller micronucleus of each individual now passes over into the other individual (*G*) while the larger one is retained. The two pieces, one derived from each individual, now fuse to make the fusion micronucleus (*H*). During these stages of the process the macronucleus has been undergoing fragmentation and sooner or later its parts degenerate completely. The parts, however, may linger for a considerable time and thus render difficult the interpretation of subsequent stages. Soon after the exchange of micronuclei the individuals separate and the process of conjugation itself is completed. Fusion of the micronuclei, however, initiates a series of changes covering a long period. These processes in one of the ex-conjugants are essentially as follows. The fusion micronucleus divides three times (Fig. 143, *I-M*), resulting in the formation of eight micronuclei. Of these, four enlarge and become macronuclei, while the other four remain micronuclei. The ex-conjugant then divides twice (*N-P*), each new individual receiving one micronucleus and one macronucleus. After a growth period each cell divides by fission in the ordinary manner and at intervals of 16 to 24 hours thereafter for a considerable period, when again conjugation usually occurs. The part of this process which corresponds to fertilization is the exchange of micronuclei and the formation of a new nucleus from the two parts. The repeated divisions of the cells following conjugation are to be likened to segmentation of the fertilized ovum of the metazoa.

In Vorticella and its allies there is a series of nuclear changes somewhat like that in Paramecium, but there is complete fusion of a smaller with a larger individual.

Parthenogenesis.—In an earlier part of this chapter the statement was made that sexual reproduction usually involves two parents and the fusion of two germ cells. Nevertheless it is not uncommon to find species of invertebrates among which, for considerable periods of time, no males can be found. The females produce eggs which develop into new individuals like the parent, although insemination or fertilization by spermatozoa does not occur, since no males are present. By their origin and maturation the cells giving rise to new individuals are ova, hence the method is obviously a sexual one. From the fact that only one parent is concerned it is said to be *unisexual* reproduction, more commonly known as *parthenogenesis*. There are many animals which employ parthenogenesis. Among these may be mentioned various species of rotifers, many small Crustacea, and insects of certain orders. Some insects which employ parthenogenesis are the well-known plant lice or aphids, and many ants, bees, and wasps. The method has also been observed in a few moths, a few of the scale insects, and commonly among

the flower-inhabiting insects known as thrips. The life cycles of some of these species are remarkable.

The females of many parthenogenetic species produce, for a number of generations, only females. At intervals, frequently in the fall, males are also produced which fertilize the eggs. These zygotes usually differ from the unfertilized eggs in being provided with hard shells and in being resistant to the rigors of a winter season. The fertilized eggs hatch in the spring into parthenogenetic females which repeat the cycle as outlined. Many species of aphids and of the lower Crustacea have cycles of this type. In certain insects the bisexual reproductive phase is apparently entirely omitted and reproduction is exclusively parthenogenetic. Thus the black flower thrips, *Anthothrips niger*, the brown chrysanthemum aphid, *Macrosiphum sanborni*, many species of scale insects and some gall-producing insects never produce males. In the ants, bees and wasps, both males and females are usually produced. The female lays both fertilized and unfertilized eggs, in some way controlling fertilization of the eggs by the release or retention of spermatozoa stored in the seminal receptacles. Among bees the males (drones) are derived from unfertilized eggs, the females (queens and workers) from fertilized eggs.

Fertilization, where it occurs, has a dual function, (1) that of stimulating the egg to develop, and (2) that of introducing the hereditary properties of the male parent. In parthenogenesis there is only one parent, hence no paternal qualities can be transmitted, and the eggs are able for some reason to start development without any stimulus from a spermatozoön.

Artificial Parthenogenesis.—The exact nature of sexual reproduction has been a matter of speculation and in recent years a matter of painstaking research. The researches of Loeb and others upon artificial stimulation of development of the egg have thrown considerable light upon the effect of the spermatozoön upon the egg. Development of the egg induced by artificial means is called *artifical parthenogenesis*.

Loeb found that if the unfertilized eggs of a sea urchin be placed for about two hours in sea water whose osmotic pressure has been increased a definite amount by increasing the proportion of salts to water, and then replaced in normal sea water, the eggs segment and develop into swimming larvæ. Other methods were employed for the initiation of development of eggs of other animals, as starfish, mollusks, and annelids. Some of the parthenogenetic agents used are the fatty acids, saponin, solanin, bile salts, the solvents of lipoids (as benzol, toluol, amylene, chloroform, aldehyde, ether, alcohols, etc.), bases, salts, hypertonicity and hypotonicity of solutions, and rise in temperature. Serum extracts of cells or of spermatozoa of unrelated species or even contact with living foreign spermatozoa as those of the shark, fish or fowl sometimes cause eggs to

segment. Shaking the eggs of certain marine animals, stroking the eggs of moths, and pricking the egg of a frog with a fine needle have also been shown to cause development. In most of these instances development does not proceed very far, but the problem of fertilization is in part concerned with the mere initiation of development.

The immediate cause of development of an artificially parthenogenetic egg is uncertain. In normal fertilization of an egg by a spermatozoön, it has been shown that the rate of oxidation of the egg increases about 400 to 600 per cent, and there is much to indicate that the agents inducing artificial parthenogenesis also increase oxidation. Even if the increase of oxidation is not the real cause of development, that cause is almost certainly some chemical or physical phenomenon. It is known in some cases that the agents which artificially cause segmentation of the ovum alter the colloidal state of the protoplasm. The protoplasm becomes stiffer (more viscous), and this change is followed by segmentation. After the start of each division the protoplasm becomes more liquid, but more viscous again at the beginning of the succeeding division. Similar changes occur at the time of normal fertilization by a spermatozoön, suggesting that the artificial agents operate in the same way as does the spermatozoön.

Pædogenesis.—Sexual reproduction is usually carried on only by adults, though this is not always the case, for there are certain species whose members have the remarkable power of reproducing sexually while they are in the larval[1] state. This reproduction by a larval animal is called *pædogenesis*. Pædogenesis may be of two types, parthenogenetic or bisexual.

Parthenogenetic pædogenesis occurs in certain species of flies. The larvæ in these species (Fig. 144) produce ova which develop by parthenogenesis into larvæ before the oviducts are present. The latter generation of larvæ escape from the parent larva by rupture of the body wall. This results in the death of the parent. Several generations may be produced in this fashion; then the larvæ of the last generation pupate and emerge as normal adult males and females.

In the succeeding instances pædogenesis of the bisexual type occurs. The ctenophore *Bolina hydatina* while still in the larval condition becomes sexually mature and its gonads produce eggs or spermatozoa. Fertilized eggs develop in the usual manner. The larva eventually assumes the adult condition and the gonads, which had degenerated, again attain sexual maturity and produce eggs or spermatozoa. Among vertebrates the well-known axolotl, *Ambystoma tigrinum* or tiger salamander, under certain conditions attains sexual maturity and breeds while it is still in

[1] A larva is a young independent individual which differs from the adult in the possession of organs not possessed by the adult, or in lacking certain organs which are present in the adult (for example, a frog tadpole).

the larval form. In some of the Mexican lakes this is said to be the usual occurrence. In Kansas and Nebraska this method of production in *Ambystoma tigrinum* has been observed but rarely, while in many localities it probably does not occur at all.

Hermaphroditism.—Most animals possess either male or female organs of reproduction but not both. This is the condition in the great majority of species of the metazoa. Species which have separate sexes are said to be *diœcious* (living in two houses) while those species whose individuals produce both eggs and spermatozoa are called *monœcious* (living in one house). Individuals with both male and female organs are known as *hermaphrodites* and they exhibit the phenomenon called *hermaphroditism*. True hermaphroditism is rare among vertebrates but traces of it are found in certain cyclostomes and commonly among Amphibia. The invertebrates present many cases of true hermaphroditism. *Hydra viridissima* and *H. vulgaris* are well known examples. Most species of flatworms including the turbellarians, cestodes or tape-worms, and trematodes or flukes, are hermaphroditic. A few species of nematodes or roundworms and most snails

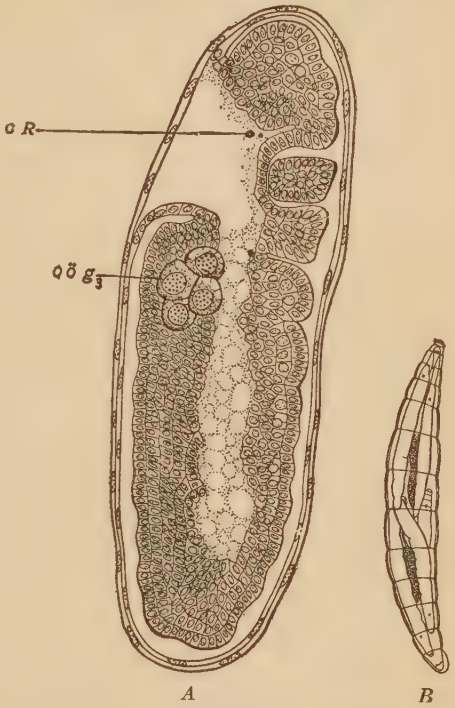

FIG. 144.—Pædogenesis in the fly Miastor. *A*, sagittal section (greatly enlarged) through an embryo of *Miastor americana*, showing four oögonia (*oög*3); *B*, mother larva of Miastor with young pædogenetic larvæ. (*A from Hegner's Germ Cell Cycle, The Macmillan Company; B from Folsom after Pagenstecher.*)

FIG. 145.—Earthworms, *Helodrilus fœtidus* (Savigny), copulating. (*After Foot.*)

are also hermaphroditic. In many species the spermatozoa are produced first and later the ova, but in some species this condition is reversed. By developing the sexual products at different times cross-fertilization, that is,

fertilization of eggs by spermatozoa from another individual, is assured. In the earthworm, eggs and spermatozoa are produced in the same individual and at the same time. Cross-fertilization is assured in this case by the arrangement of the generative organs and by the method of mating.

Mating in the earthworms may occur under the surface of the soil, or in a compost heap as in the case of *Helodrilus fœtidus* (the manure worm), or above the soil as in *Lumbricus terrestris*, the large worm generally used for laboratory dissection. In these species the bodies of the two worms are closely applied by their ventral surfaces, the heads pointing in opposite directions and the thickened band or *clitellum* of each worm approximately opposite segments 7 to 12 of the other worm (Fig. 145). In this position each worm secretes a *slime tube* which encircles its body from about segment 8 to segment 33 or even as far back as 39. In some instances, at least, the slime tubes of the two worms seem to be independent of each other. In the region of the clitellum of each worm thickened rings of the slime tube encircle both worms and bind them closely together. The spermatozoa are discharged from the *spermaducal pores* into the space bounded by the slime tube and the body of the worm. Here the spermatozoa form into irregular masses or *spermatophores* which are carried backward within the slime tube by the muscular contractions of the body of the worms and finally are picked up by the seminal receptacles of the other member of the pair. Transfer of spermatozoa in the worm is supposed to be a reciprocal act but it is not definitely known whether both worms discharge spermatozoa at the same time, or at different times during one copulative act, or at different matings. While still bound together by the mucous bands the worms may each produce a cocoon which surrounds its body. This is accomplished by the hardening of a secretion poured out by the gland cells of the clitellum. The eggs are conveyed to the cocoon by the slime tubes while the cocoons are still in position about the clitellum. No spermatozoa are present in the cocoon at this time, but they are discharged as the cocoons pass the openings of the seminal receptacles on segments 9 and 10, or possibly spermatozoa are conveyed to the cocoons by the slime tubes while the cocoon is passing forward. Fertilization occurs after the deposition of the cocoon. To deposit the cocoon the worm creeps backward out of the slime tubes and the cocoon. Thus the cocoon is usually left surrounded by a part of the slime tube (Fig. 146). As soon as the cocoon passes the head of the worm its elastic ends contract and sharply close the openings. Development of the eggs occurs within the cocoon.

From observations by Miss Foot on worms in captivity it seems that mating may be followed at intervals by the formation of several successive cocoons. A slime tube (Fig. 147) and cocoon are formed much as in worms that have just mated. The cocoon is formed about the clitellum and the deposition of the eggs and spermatozoa occurs as

described above. She found that *Helodrilus fœtidus* when kept singly in captivity formed cocoons about every third day after mating, sometimes until as many as 10 cocoons had been formed. At the close of this period the clitellum was much reduced in size and the seminal receptacles nearly empty.

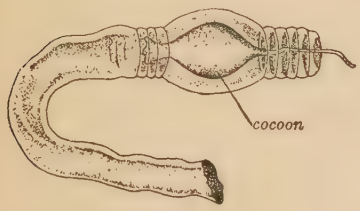

FIG. 146.—Slime tube of the earthworm *Helodrilus fœtidus* with cocoon. (*After Foot.*)

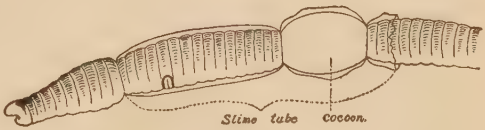

FIG. 147.—Slime tube and cocoon in process of formation by a single worm. (*After Foot and Strobell.*)

The arrangement of the male and female reproductive organs of the earthworm is shown diagrammatically in Fig. 148. The male organs are two pairs of *testes*, three pairs of *seminal vesicles* and one pair of *vasa deferentia*. The testes (Fig. 148) imbedded in the bases of larger organs, the seminal vesicles, in which the spermatozoa undergo their later development and await the time of copulation. Delicate tubes, the

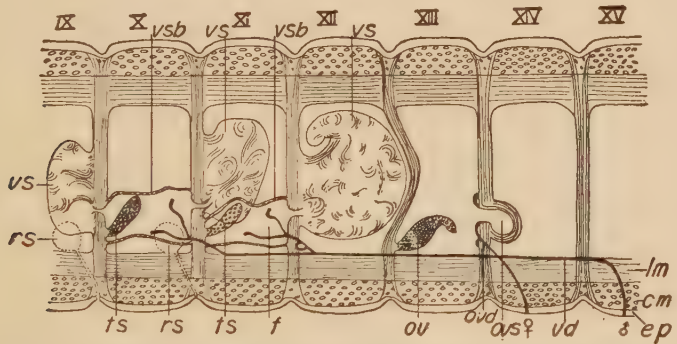

FIG. 148.—Reproductive organs of the earthworm, schematic representation of the side view. *IX–XV*, numbers of somites; *cm*, circular muscles; *ep*, epithelium; *f*, funnel of vas deferens; *lm*, longitudinal muscles; *ov*, ovary; *ovd*, oviduct; *ovs*, ovisac; *rs*, receptaculum seminis; *ts*, testis; *vd*, vas deferens; *vs*, vesicula seminalis; *vsb*, base of vesicula seminalis; ♀, opening of oviduct; ♂, opening of vas deferens. (*Modified from Hesse.*)

vasa deferentia, which originate in funnels in the base of the seminal vesicles and which open to the surface in the common earthworm on somite 15 conduct the spermatozoa to the exterior. The same worm also possesses a set of female reproductive organs consisting of one pair each of *ovaries*, *ovisacs* and *oviducts*, and two pairs of *receptacula seminis*. The eggs are discharged from the ovaries into the cœlomic cavity and are collected in the ovisacs, where they remain until they finally pass down

the oviducts to the exterior. The two pairs of receptacula seminis are sac-like organs in which spermatozoa are received at copulation and stored for future use in fertilizing the ova. They are located anterior to the male organs and have no ducts communicating with the other parts of the female reproductive system.

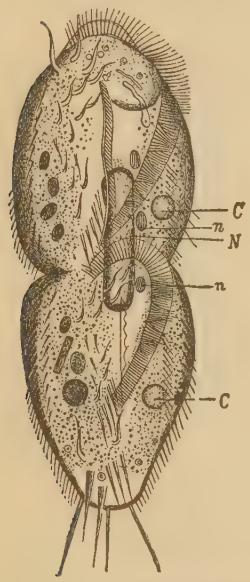

FIG. 1.—*Stylonychia mytilus* dividing. *C*, contractile vacuole; *N*, macronucleus; *n*, micronuclei. (*From Sedgwick, after Stein. Courtesy of The Macmillan Company.*)

While in the earthworm and in some other hermaphroditic species an elaborate mechanism insures cross-fertilization, in other hermaphroditic species no such devices exist and indeed, self-fertilization (fertilization of eggs by spermatozoa of the same individual) is well known either as a regular or occasional occurence. Some plants as wheat and beans regularly self-fertilize. Other plants as the violet produce some flowers which are regularly cross-fertilized and others which can only be self-fertilized. Among parasitic flatworms (the cestodes and trematodes) both cross- and self-fertilization have been observed.

Asexual Reproduction: Fission.—Fission is a common reproductive method among the protozoa, but occurs less commonly among the metazoa. The essentials of fission are that the parent cell or the parent body (if a metazoön) is divided into approximately equal parts, each of which grows and regenerates the missing parts and thus comes to resemble the parent. In *binary* fission (division into two equal parts) as it occurs in the protozoa the parent disappears as an individual and two new individuals take its place. The plane of fission may be longitudinal or transverse. Transverse fission, that is, division perpendicular to the long axis, is the more common. It is illustrated in Fig. 149 which shows Stylonychia in division. Even in forms like Vorticella (Fig. 150), in which fission appears to be longitudinal, the division is really transverse, since the ciliated disk which seems to be the end of the cell is morphologically its ventral surface.

FIG. 150.—Vorticella in division. (*From Kent after Greef.*)

Fission involves the nucleus as well as the cytoplasm. Structures which extend across the plane of fission are halved and the missing portion regenerated. Other structures go with that portion in which they are located before fission, and corresponding structures arise anew in the other portion. Thus in species with two contractile vacuoles, one placed anteriorly, the other posteriorly, one vacuole goes to each new individual and a second vacuole arises anew in each. In Stylonychia and many

other forms the ciliary apparatus is developed afresh, sometimes before fission is completed. In forms which have both macro- and micronuclei, both nuclei elongate and finally divide, a half going to each new individual. After the separation into two individuals regeneration is completed and each individual grows in size. In the protozoan parasite *Opalina ranarum* division of the nucleus proceeds until many nuclei, even as many as a hundred or more, are produced, then the cytoplasm divides by successive binary fissions to form as many little cells as there were nuclei. Encystment of the small individuals frequently follows these divisions. In Paramecium, when well fed, fission occurs once in about 16 to 24 hours.

In the reproduction of certain Sporozoa (parasitic protozoa reproducing by spores) the nucleus of a large cell may divide many times without the division of the cytoplasm. Later the cytoplasm fragments, not by successive binary fissions but by many simultaneous divisions, into as many pieces as there are nuclei, thus forming a number of small cells at the same moment. This process is sometimes called *multiple fission*, and sometimes *sporulation*. It occurs regularly in the complicated life histories of the organism of malaria and in the coccidia.

Fission also occurs in certain of the worms, as the Turbellaria and some species of nemerteans. These particular instances are also referred to by some zoölogists as *budding*.

Budding.—A simple and common mode of asexual reproduction is that of budding. The bud starts as a protrusion of protoplasm in a small area of the surface of a protozoan cell or as a localized proliferation of cells in a multicellular animal. The protuberance grows until it assumes the form and perhaps the size of the parent. It usually develops organs similar to those of the parent and either becomes independent of, or remains attached to, the parent. Budding is a rare reproductive process among the protozoa but is common in certain groups of the metazoa. In the latter, buds may be developed within the body or on the external surface, and some species, such as the freshwater sponges and freshwater bryozoa, produce buds in both situations at the same time.

Internal Budding.—In addition to the external buds whose limits are indefinite, the freshwater sponges produce large numbers of minute internal buds called *gemmules*. A gemmule is a small group of cells produced by proliferation of cells, chiefly somatic, within the mesoglœa (gelatinous material) of the sponge. These cells are enclosed within a dense layer of material in which spicules of peculiar types may be imbedded. Gemmules are usually produced in abundance during summer and fall. When the body of the sponge disintegrates the gemmules (Fig. 151) are left clinging to the log or stone to which the sponge was attached. They may remain here or they may be transported considerable distances by water currents or perhaps on the feet or beaks of

water birds. With the return of favorable conditions the bud enclosed within the outer coating of the gemmule begins to develop. In some manner it removes the plug which closes the aperture of the covering and the minute sponge emerges. It soon assumes the form and appear-

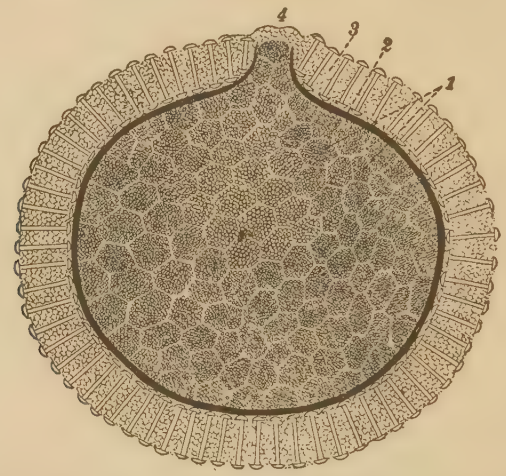

Fig. 151.—Gemmule of the freshwater sponge Ephydatia, in schematic cross-section. 1, cells; 2, chitinous case; 3, shell with amphidisc spicules; 4, foraminal aperture. (*From Hesse and Doflein.*)

ance of a minute sponge (Fig. 152) which by growth and external budding becomes the large sponge as it is found during the summer and fall. The gemmule of the sponge is, therefore, not only a medium for multiplying

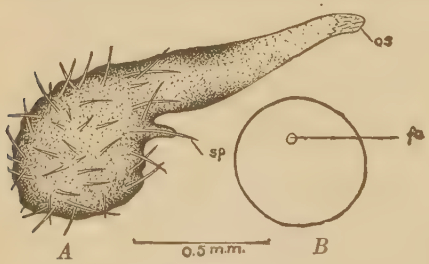

Fig. 152.

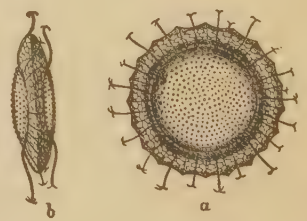

Fig. 153.

Fig. 152.—Origin of sponge by asexual reproduction. *A*, young freshwater sponge recently emerged from a gemmule; *B*, outline sketch of the gemmule of the same species; *fa*, foraminal aperture; *os*, osculum; *sp*, spicule. The scale beside the figures indicates their size.

Fig. 153.—Statoblasts of *Cristatella mucedo*. *a*, view from flat side; *b*, edge view. (*From Sedgwick, after Allman. Courtesy of The Macmillan Company.*)

the number of individuals, but also a means of dispersal of the species and of surviving the vicissitudes of winter.

The Bryozoa (moss animals) living in fresh water also produce internal buds which when enclosed in a dense protective covering are

called *statoblasts*. A statoblast of *Cristatella mucedo* is shown in Fig. 153. Bryozoa occur abundantly in lakes, ponds, and rivers and their statoblasts are produced in great numbers. These are released and scattered by currents of water. Some statoblasts become attached to the surface of logs or water plants and soon give rise to new colonies while others persist over winter before releasing the young individual from which a colony arises by budding.

External Budding.—External budding is a much more common type of reproduction than internal budding. In some species when the bud has attained a certain state of development the bud separates from the parent and thereafter leads an independent existence. This is the primitive method of budding. It is illustrated by the common Hydra and most species of annelid worms which produce buds. There are, however, numerous species of metazoa which produce buds that remain attached to the parent, and in this manner organic colonies are formed.

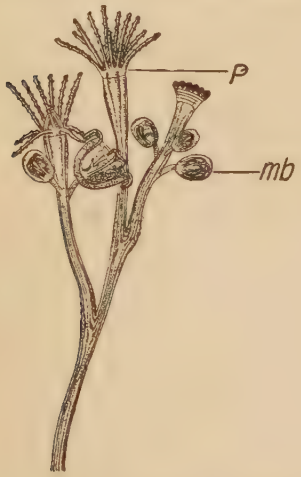

FIG. 154.—The hydroid, *Bougainvillea ramosa*, portion of a colony. *p*, polyp; *mb*, medusa bud. (*After Allman.*)

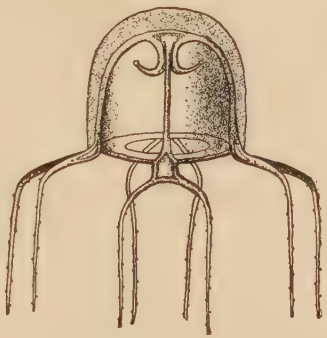

FIG. 155.—Medusa of *Bougainvillea ramosa* freed from the colony, enlarged more than Fig. 154. (*After Allman.*)

Colonies in the Metazoa.—The formation of organic colonies occurs among a few groups of the metazoa, namely, the Porifera, Cœlenterata, Bryozoa, Cestoda, Annelida (rarely), and Tunicata. Among the Cœlenterata the Hydrozoa furnish classical examples of colony formation with differentiation of individuals. Bougainvillea, Obelia, and Physalia may be taken as representatives.

Bougainvillea ramosa (Fig. 154) forms a colony with a much branched *cœnosarc* (interior cellular portion) bearing at the ends of the branches flower-like zooids, called *polyps* or *hydranths*. The polyps are each provided with a *hypostome* a conical projection at the distal end, around which is a circlet of *tentacles*. The cœnosarc is surrounded by the *perisarc*, a tough, lifeless cuticle secreted by the cells of the cœnosarc. The colony

arises from a branched root-like structure, the *hydrorhiza*, which is attached to a solid body such as a rock or log. This colony is produced by budding without separation of the buds from the parent. From the stalks of many of the polyps, *medusæ* (jellyfishes) are formed by budding. Medusæ do not resemble polyps but are bell-shaped individuals (Fig. 155) which after maturity become separated from the colony and swim freely in the water by means of rhythmic contractions of the bell. Each medusa produces eggs or spermatozoa. The fertilized egg develops into a ciliated free-swimming embryo which eventually attaches itself by one end to a rock and develops into a polyp. This polyp puts forth buds and thus a new colony is formed.

Obelia forms a colony somewhat resembling Bougainvillea. In Obelia, however, the medusa buds are produced by budding from the stalks of certain individuals (*gonangia*) which, unlike polyps, have no tentacles. Each *gonangium* is enclosed in a swollen chitinous sheath, the *gonotheca*. Obelia is thus composed of three types of individuals, two of which are sessile and incapable of sexual reproduction, while the other is a sexual free-swimming form.

Species which, like Obelia, exhibit several forms of body are called *polymorphic* (literally of many forms), and this condition is denoted by the term *polymorphism*. In Obelia, as in many other hydroids, polymorphism is accompanied in the life cycle by an alternation of asexual and sexual modes of reproduction. The individuals of one type reproduce sexually, those of the remaining types asexually. Such a combination of polymorphism with sexual and asexual reproduction is called *metagenesis*. Metagenesis is common among cœlenterates but is rare outside this group.

The remarkable examples of colony formation and metagenesis, accompanied by division of labor among the types of individuals that reproduce asexually, occur among the Siphonophora, one of the orders of Hydrozoa. These are free-swimming colonies of varying complexity. Each siphonophore colony (Fig. 156) consists of a common tube of cœnosarc which bears at one end a *pneumatophore* or float and along its length zooids of various forms. The float is the expanded end of the cœnosarcal tube. It generally contains gas and serves to support the colony which hangs freely in the water. Near the float is a group of swimming bells (*nectocalyces*) which resemble medusæ and whose function it is to propel the colony through the water by their alternate contraction and expansion. At intervals below the swimming bells occur *bracts* or covering scales, feeding polyps which ingest the prey and digest it for the entire colony, sensory polyps which in some species at least also serve as digestive organs, *tentacles* (defensive and offensive individuals) provided with nematocysts, and *gonophores* (reproductive zooids) with or without bells. A first examination of a siphonophore

might lead to the conclusion that it is a complex individual with half a dozen kinds of organs. By a careful study of selected forms, however, and by means of a comparison of these with such forms as Obelia and Hydractinia and other Hydrozoa, it may be determined that each type of zooid which in a siphonophore resembles and functions as an organ is really a much modified individual, either polyp or medusa. In certain species the bracts contain remains of *radial canals* which are charac-

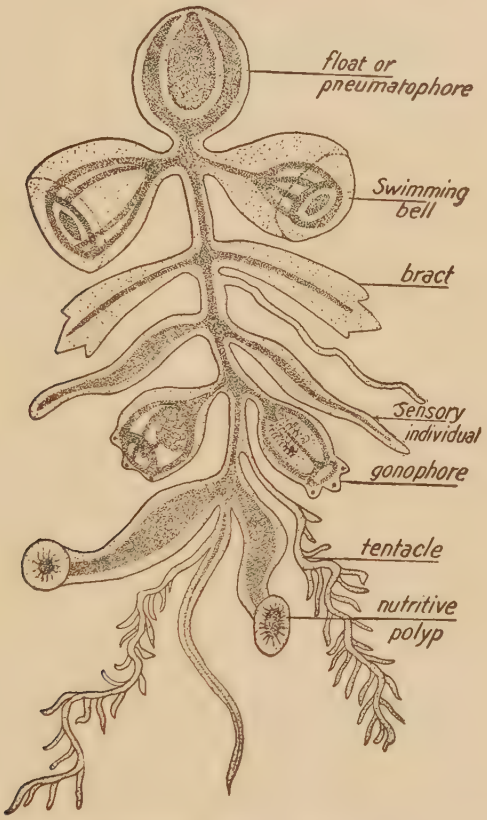

FIG. 156.—Diagram of a siphonophore colony composed of six kinds of individuals. (*Modified from Fleischmann.*)

teristic of medusæ. The bracts, swimming bells, and gonophores are constructed on a medusoid plan while the feeding polyps, sensory polyps and tentacles are constructed on the polyp plan. In a few species the gonophores may separate from the colony, as do the medusæ in typical hydroids, but usually they remain attached.

The Portuguese man-of-war, Physalia (Fig. 157), differs from the generalized form described above in possessing a float which sits high above the water and serves as a sail. It has no swimming bells or bracts.

Among the metazoa the formation of colonies (as distinct from societies such as exist among ants, wasps, and bees) occurs only in those groups which employ an asexual mode of reproduction such as budding or fission. Animals which employ the sexual method of reproduction alone do not form colonies.

FIG. 157.—*Physalia*, the Portuguese man-of-war, drawn from live animal floating on the surface of the sea. *cr*, crest; *p*, polyp; *pn*, pneumatophore; *t*, tentacle. (*From Parker and Haswell's Textbook of Zoölogy, after Huxley.*)

Origin of Colony Formation.—The colonies described above are organic colonies since each is an intimate union of individuals of the same species. Such colonies may consist of like individuals or there may be differentiation, polymorphism, and division of labor. Colony formation occurs chiefly among the less highly organized groups of animals and it is most frequent among attached forms. The formation of colonies may be of advantage to the species in that it permits members of the species to occupy as solid masses positions which are favorable to their life processes. This is true of the corals which by reason of their method of

building solid skeletal structures as an activity of the whole colony are enabled to thrive in situations where single polyps could not do well. Colony formation, especially when it involves polymorphism and division of labor, may have made for greater efficiency in the performance of certain functions, but it should not be considered that efficiency is a goal toward which species have striven. Colony formation seems rather to have been more or less of an accident made possible because of the presence of an asexual reproductive method. It seems not improbable that its origin was due in some groups to a failure of the mechanism by which budding or fission is normally completed.

Limits of Asexual Reproduction.—Asexual reproduction occurs only among the lower forms of animal life. It never occurs among vertebrate animals, although it does occur among the ascidians which are placed in the phylum to which vertebrates are also assigned. It also does not occur in the following phyla of invertebrates: the Nemathelminthes (roundworms), the Rotifera (rotifers), Echinodermata (starfishes, sea urchins, sea cucumbers, etc.), the Mollusca (cuttlefishes, squids, nautiloids, clams, oysters, and snails), and the Arthropoda (lobsters, shrimps, crayfishes, insects, and spiders). Even in some of the phyla in which examples of asexual reproduction occur there are many species, indeed some entire classes and orders, in which asexual reproduction is never found. The method is, however, widespread among animals, and in many species (oligochæte worms, Hydra and the protozoa) it may occur for many generations without the intervention of the sexual method. From its occurrence principally in the lower animals, and from the comparative simplicity of the process, asexual reproduction must be regarded as the primitive method of forming new individuals.

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CHAPTER X

THE BREEDING HABITS OF ANIMALS

Reproduction in which both sexes are involved is dependent upon the uniting of the germ cells, proper conditions for the development of the fertilized egg, and conditions suitable for the development of the immature animal. The parents do more or less to insure the union of the germ cells, to provide proper conditions for the development of the fertilized egg, to guard against accident to the immature offspring, and to help it over the period of its own helplessness. These services of the parents are habitual, and are known collectively as "breeding habits." A considerable amount of data on breeding habits has been accumulated by zoölogists, but this is widely scattered in the literature and is very fragmentary. The habits of relatively few forms are known in detail.

Breeding habits in the animal kingdom are exceedingly varied. There are two apparent reasons for this variety. First, different forms have different modes of life, and the breeding habits must be suited to the manner of living if they are to accomplish their purpose. Second, the increasing complexity attained in the higher forms of life apparently necessitates in them a longer period of prenatal development. At least, the development before birth or hatching is longer in the complex forms than in the simpler ones, and the length of time required for this development seems to be related to the place of the forms in the animal scale. There may be other reasons than these two; but whatever the explanation of them, the breeding habits of animals exhibit very great diversity. The differences in habits are not characters that distinguish large groups, as phyla[1] and classes, from one another; for within these and smaller groups there is considerable dissimilarity in breeding habits. Even the several species of a single genus, especially a large genus like Hyla which includes the tree frogs, may employ very different means of assisting the processes of reproduction and development. Because of this diversity no attempt will be made to describe in detail the various breeding habits of animals. The endeavor will rather be to bring order out of seeming chaos, to classify and summarize, and to introduce just enough detail to illustrate in concrete manner the several types of breeding behavior. As a foundation for the discussion of breeding habits the urinogenital systems are briefly reviewed first, then habits dealing with the union of the germ

[1] For the significance of the terms phylum, class and genus, see the chapter on Taxonomy.

cells are described, after which those relating to the fertilized eggs and the young are discussed

Urinogenital Systems.—In vertebrate animals the reproductive and excretory systems are intimately connected and together they comprise the *urinogenital* system. The excretory system of the frog has already been described. In both sexes of the frog the gonads develop ventrally to the kidneys and here they hang suspended in loops of peritoneum. This relation is most plainly seen in the male and in young females whose ovaries have not yet become voluminous.

The oviducts are coiled tubes dorsal to the ovaries (Fig. 158). Each oviduct takes its origin in a ciliated funnel which lies just dorsal to the

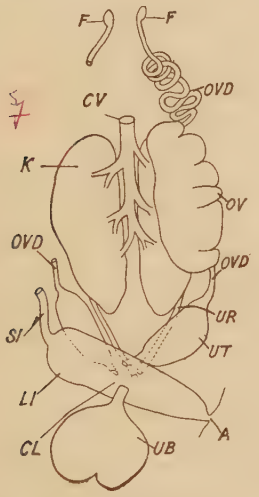

Fig. 158.

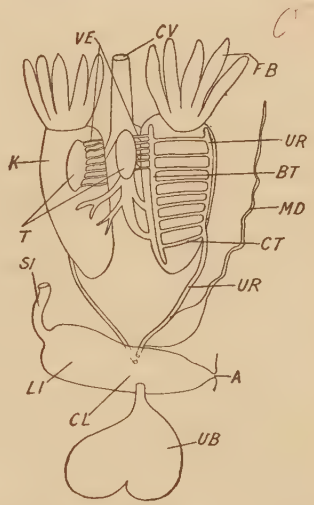

Fig. 159.

Fig. 158.—Urinogenital system of female frog, diagrammatic. *A*, anus; *CL*, cloaca; *CV*, post caval vein; *F*, funnel of oviduct; *K*, kidney; *LI*, large intestine; *OV*, ovary; *OVD*, oviduct; *SI*, small intestine; *UB*, urinary bladder; *UR*, ureter; *UT*, uterus.

Fig. 159.—Urinogenital system of male frog, diagrammatic. The kidney at the left is in surface view, at the right in diagrammatic optical section. *A*, anus; *BT*, Bidder's tube; *CL*, cloaca; *CT*, collecting tubule; *CV*, postcaval vein; *FB*, fat bodies; *K*, kidney; *LI*, large intestine; *MD*, Muellerian duct; *SI*, small intestine; *T*, testes; *UB*, urinary bladder; *UR*, ureter; *VE*, vasa efferentia.

heart and at the extreme anterior end of the cœlomic cavity. The posterior end of each oviduct is transformed into a thin-walled distensible bag, the *uterus*, which is connected by means of a narrow passage with the cloaca, in the same region as the opening of the ureter. The walls of the uterus and the *ureter* become united side by side in their lower courses but their cavities remain distinct. Eggs are released into the body cavity by ruptures in the peritoneum covering the ovaries. They are carried forward to the funnels of the oviducts by the currents caused by general body movements, assisted by pressure of the fore arms of the

clasping male. Currents are also produced by the strong beating of the cilia which line the funnels of the oviducts. These currents induced by the cilia sweep the eggs and other matter into the open funnels and down the oviducts. The remainder of the path to the exterior is indicated by the structure and arrangement of the organs.

In the male frog (Fig. 159) the testes are connected to the kidneys by means of fine ducts, the *vasa efferentia*. These fine ducts penetrate into the kidney and open into a longitudinal canal (*Bidder's canal*) which is a long tube running lengthwise of each kidney near its median border. Bidder's canal is connected with the ureter by means of a series of *collecting tubules* into which the uriniferous tubules also open. Spermatozoa in the frog must therefore pass through the vasa efferentia, Bidder's canal, the collecting tubules, the ureter and cloaca on their way to the exterior. In some species of frogs, the lower end of the ureter in the male may be expanded into a *seminal vesicle* in which spermatozoa are stored until they are emitted at the time of breeding.

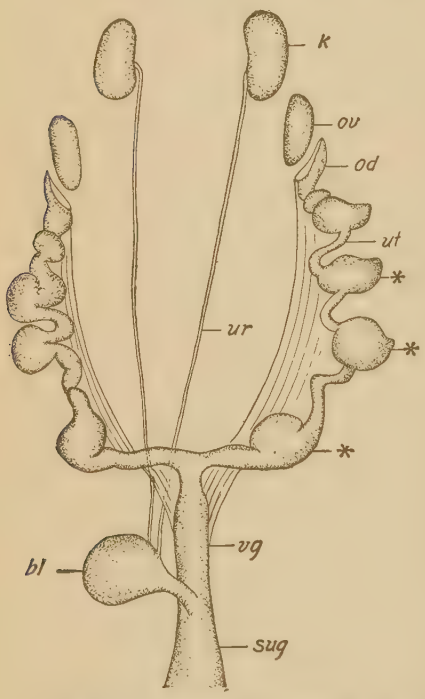

FIG. 160.—Urinogenital system of a female mammal having a bicornuate uterus, somewhat schematic. *bl*, urinary bladder; *k*, kidney; *od*, oviduct; *ov*, ovary; *sug*, urinogenital sinus; *ur*, ureter; *ut*, uterus; *vg*, vagina; *, position of embryos. (*Modified from Wiedersheim.*)

A comparison of the reproductive systems of male and female frogs reveals that in the female the reproductive organs are less intimately connected with the excretory organs than in the male. In reptiles and birds, the genital system, especially in the male, is in some respects more distinct from the excretory system than it is in the Amphibia. In both of these classes, as in the Amphibia, both excretory and genital systems discharge into the cloaca.

In most mammals, the genital and excretory systems open to the exterior through a common opening which is separate from the anal opening. In the female, the funnel of the oviduct is close to the ovary, but is not connected with it. The oviduct opens into the uterus in which the young are retained and nourished until birth. The form of the uterus differs in the different groups of mammals. That illustrated in

Fig. 160 is common among the carnivores, rodents, and others which bring forth young in litters. The uterus is connected to the exterior by the vagina which is the copulation passage. The urinary bladder, which belongs to the excretory system, is connected to the lower portion of the vagina by means of the urethra. In some mammals there are accessory glands in connection with the female urinogenital system. In the male, the testes are connected by means of the *vasa deferentia* (singular, *vas deferens*) with the urethra, which extends from the urinary bladder through the *penis*. There are usually accessory glands.

Methods of Insuring Fertilization.—Since bisexual reproduction is the union of protoplasm from two individuals or the union of differentiated cells from the same parent the first essential is that the uniting elements be brought together. The general act of bringing the germ cells or their equivalents together has often been termed *copulation*. The term copulation, however, as previously stated, is not usually applied to the protozoa, since these simple animals do not possess germ cells, as distinct from somatic cells. The word copulation is in practice used only for the metazoa, in which true germ cells are formed, leaving the union of protozoa for nuclear exchange to be designated by the term conjugation, or fusion if there is complete union of their bodies. Furthermore, while frequently used in a general sense to designate the act of bringing the germ cells together, the word copulation is more accurately used when restricted to the act of introducing the male elements into the body of the female in those forms which have internal fertilization. The act of clasping without copulation is specifically known as *amplexus*.

Fertilization in Hermaphroditic Animals.—A relatively small number of animals, among them some sponges, Hydra and a few of its relatives, worms, and snails, are hermaphroditic (Fig. 161). Among these hermaphroditic forms, as in many sponges, the production of ova usually predominates in some individuals, the production of spermatozoa in others. In many hermaphroditic species the male and female elements are produced at different times, a condition known as *dichogamy*. When, as in most tunicates, the hermaphroditic animals are regularly female at first and later male, they are said to be *protogynous*. Others, like the mollusk Crepidula, are first male and then female and are said to be *protandrous*. Regarding hermaphroditism in general it may be said that it is more common among the invertebrates than among the vertebrates; that it is the normal condition in tunicates and a few fishes; that it is occasional in other fishes and in the amphibians; and that it occurs as an abnormal condition in reptiles, birds and mammals. In most of the cases of hermaphroditism in the higher animals the individuals do not, however, function as both sexes. They may be so abnormal as not to function as either sex. Concerning such forms, of course, there can be no discussion of methods of insuring fertilization.

Only a few of the hermaphroditic animals, for example some nematode worms and the parasite Sacculina, are self-fertilizing. In self-fertilizing forms the eggs are usually fertilized within the body and there is no act of copulation. In hermaphrodites that are not self-fertilizing the eggs are in some cases fertilized within, in other cases outside of the body, and various methods of insuring fertilization are to be observed. In hermaphroditic hydras the spermatozoa are shed into the water and find

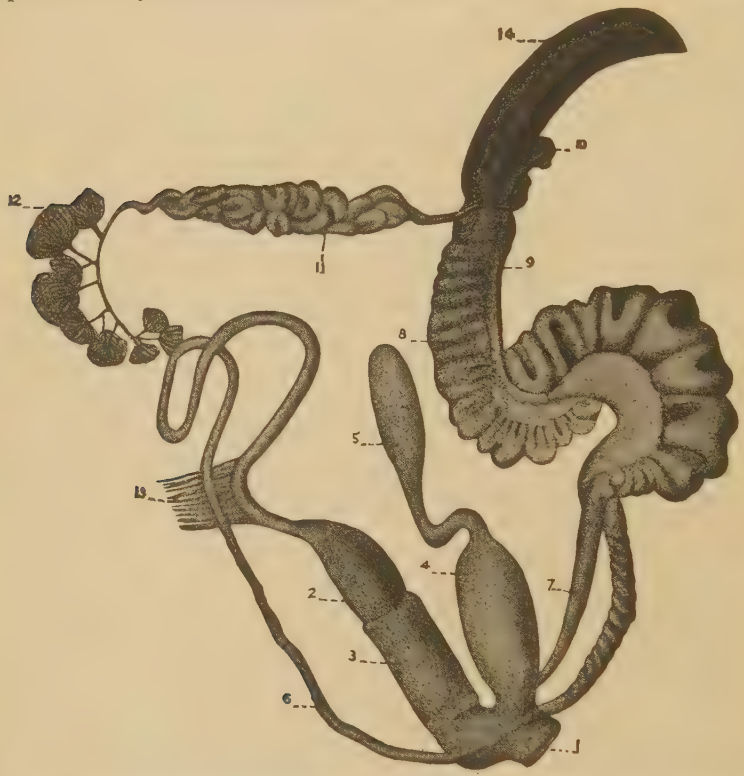

Fig. 161.—Genital organs of a hermaphrodite animal, a common land snail *Polygyra albolabris* (Say). Note that some of the organs are characteristic of a male, others of a female. 1, atrium; 2, penis; 3, prepuce; 4, vagina; 5, spermatheca; 6, vas deferens; 7, free oviduct; 8, uterus; 9, spermatic duct; 10, talon; 11, hermaphroditic duct; 12, hermaphroditic gland; 13, penis retractor; 14, albumen gland.

the ova, still within the body, largely by chance, perhaps assisted by chemical attraction. In the earthworm, on the contrary, there is an elaborate copulatory process and capsule formation, as described in the preceding chapter.

Fertilization in Dicœcious Species.—In many aquatic animals the sexual elements or at least the spermatozoa are simply discharged into the water and the germ cells come together by chance. Thus in the jellyfishes the spermatozoa are liberated into the water, and may or may

not happen to meet the eggs, which are retained in the ovary of the female. In other animals there is congregation of the sexes at the breeding time and the eggs and spermatozoa are liberated in proximity. Starfishes and sea urchins periodically congregate in this manner. The close association of the sexes thus caused undoubtedly greatly favors the meeting of the germ cells, but still leaves to chance an important rôle, and many eggs are probably never fertilized. The giant salamander Cryptobranchus is a form that congregates with its fellows at the breeding season. In certain other salamanders, those of the genus Ambystoma, the male deposits the spermatozoa in a naked, nearly spherical mass resting on a gelatinous stalk which is attached to a leaf or some other object in the water. This structure, including the stalk, is called a *spermatophore* (Fig. 162). The mass of spermatozoa at its top is subsequently removed by the female with the lips of the cloaca, and the eggs are fertilized within her body. There is no copulation nor amplexus among any of the forms just mentioned. Copulatory

Fig. 162.—Spermatophore of *Notophthalmus viridescens viridescens* (Raf.), the common newt of eastern North America. The stalk is a clear gelatinous substance; the apical mass (dotted in the figure) is a snowy-white mass of seminal fluid containing spermatozoa. (*After B. G. Smith.*)

Fig. 163.—Amplexus in a species of toad, *Bufo typhonius* (Linnæus). The small individual is the male, the larger the female. (*Photograph by A. G. Ruthven.*)

habits are to be found, however, among some forms in which fertilization does not take place until after the eggs are laid, as well as among those in which the eggs are fertilized within the body of the mother. Furthermore, the eggs may or may not be fertilized at the time of copulation or

amplexus. In the tailless amphibians (the frogs and toads) and some fishes, the sexes congregate during the breeding season, the male clasps the female, and the seminal fluid is poured over the eggs as they are emitted (Fig. 163). Here the fertilization occurs during or just after amplexus. In the crayfishes, however, the spermatozoa transferred during copulation are stored in a seminal receptacle in the abdomen of the female, from which they are presumably emitted to fertilize the eggs as these are laid several months later. In some of the salamanders in which the male deposits spermatophores, amplexus also occurs. Thus, in *Notophthalmus viridescens* the males clasp the females and deposit the spermatophores afterwards. In this respect these species differ from Ambystoma, mentioned above, in which there is no amplexus. In a very large number of animals there is still further insurance of fertilization, for the spermatozoa are transferred directly from the male to the female (true copulation), fertilization taking place within the body of the female. This method is employed by some parasitic worms, snails, fishes, and amphibia, and by all of the insects, reptiles, birds and mammals.

Summary of Methods of Fertilization.—Notwithstanding the confusion which this array of special devices and practices may seem to exhibit, four well-defined general types of combination of place and mode of fertilization may be recognized as follows:

1. External fertilization without amplexus. The eggs and spermatozoa are deposited freely in the water to come together by chance.

2. External fertilization with amplexus. Amplexus may occur some time before egg-laying, or the eggs may be laid during amplexus. In the former case, the eggs are fertilized by spermatozoa stored in the seminal receptacle of the female. In the latter case, they are fertilized directly by the male. In either case fertilization takes place while the eggs are being laid.

3. Internal fertilization without copulation or amplexus. The female takes into her body groups of spermatozoa previously deposited by the male.

4. Internal fertilization with copulation or amplexus. The spermatozoa are directly transferred from the male to the female (copulation) or are deposited by the male during or just after amplexus. In the latter case the female secures them immediately or after an interval.

Do the Methods of Insuring Fertilization Exhibit an Evolutionary Series?—Since some of these types of breeding behavior are plainly much more specialized than others, one might be tempted to suppose that they exhibit some sort of evolutionary sequence. That is, it might be thought that the simpler habits would be employed by the more primitive groups of animals, while the complicated methods would be adopted by the higher forms. Such appears not to be the case, however. Thus, as

pointed out above, the last of the four types of habit recognized, which involves more specialized behavior than any of the others, is employed by some parasitic worms, some snails, the insects, reptiles, birds and mammals. These groups are so diverse in structure that it is impossible to regard them as all primitive or all highly developed. Furthermore, most of the fishes and amphibia use the second and third of these methods while some members of each of these groups follow the fourth method. In general, the same breeding habits may occur in animals of widely different groups, and animals of the same group often have very different habits.

It is worthy of note, however, that among aquatic or amphibious forms the habit prevails of depositing the spermatozoa and eggs freely in the water or in immediate proximity to each other, or depositing the spermatozoa so that they can be secured later by the female; while in the groups composed mostly of land forms the habit of introducing them into the body of the female predominates. The latter method is essential to most land forms since air is fatal to the delicate sexual cells, whereas in aquatic forms the fertilized eggs at least can endure the water for a prolonged period.

Place of Development.—From the description of the methods of insuring fertilization it will be seen that the eggs may be fertilized either before or after they are laid. That is, fertilization is either internal or external. It is now to be pointed out that when fertilization is internal the eggs may be retained for a long time after fertilization, or they may be laid very soon thereafter. Whatever period of time the eggs remain in the organs of the female after fertilization is utilized in development, so that the embryo may be far advanced before it is separated from the mother, or it may have attained only an early stage of development, or development may scarcely have started. Thus, in most of the insects and in all of the birds the eggs are laid soon after fertilization. In these cases only a few divisions of the egg, or of its nucleus, have taken place at the time of oviposition, or it may not have divided even once. On the contrary, development may proceed until a well-formed embryo is produced, and then the eggs are laid; this occurs in some of the salamanders. Usually, if the eggs undergo more than a few cleavages while within the mother, they remain until a rather late larval stage, or until the form of the adult is attained. Some insects, some snakes, and the true mammals are of the last-named type.

Source of Nourishment of the Embryo.—Animals that lay their eggs are said to be *oviparous;* the eggs may be laid before fertilization, or, if after fertilization, while the embryos are still incapable of existence outside of the egg membranes. Animals that retain the embryos until with proper care they are capable of independent existence are designated *viviparous.* Of viviparous species there are two general types. In

one of these, the eggs are large and laden with yolk, from which the embryo derives its nourishment, just as in oviparous animals. The mother serves, in such cases, chiefly as a nest in which the eggs may develop. Viviparous animals in which practically the whole nourishment of the young is furnished by the egg itself are said to be *ovoviviparous*. Some reptiles are ovoviviparous (Fig. 164), the embryos being held in the oviduct of the mother until they are far advanced but receiving the food from the egg. Among insects the plant lice are ovoviviparous. The young are born at approximately the stage in which the young of related, but oviparous, insects are hatched. The second type of viviparous animal is that in which the nutrition of the embryo is obtained from the mother, whose reproductive system is then of the general type represented in Fig. 160. The blood vessels of the embryo, running through the umbilical cord and expanding in a highly vascular tissue known as the *placenta*, are brought into very close contact with the maternal blood vessels in the wall of the uterus (Fig. 165). While no blood cells pass from the vessels of the mother to those of the embryo, nutritive materials and oxygen in solution readily diffuse into the blood of the latter. Forms in which the embryo is connected with the maternal uterus by a placenta are spoken of as truly viviparous. Hydra and jellyfishes, among aquatic animals, exhibit something like viviparity, since only the spermatozoa are shed into the water. The spermatozoa find the eggs, largely by chance, while the eggs are still in the maternal ovary and penetrate the eggs in that situation, and the fertilized eggs develop there for a time. In these cases the eggs are large, and presumably contain all the necessary nourishment.

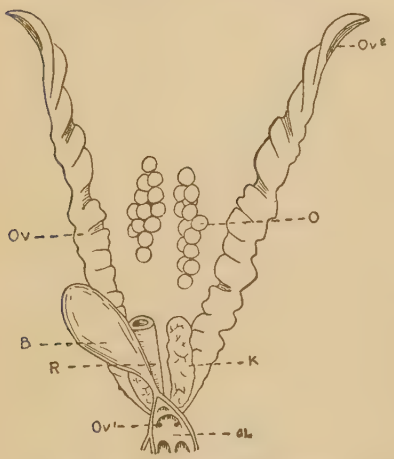

FIG. 164.—Urinogenital system of a lizard. *B*, bladder; *Cl*, cloaca; *K*, kidney; *O*, ovary; *Ov*, oviduct; Ov^1, cloacal opening of oviduct; Ov^2, abdominal opening of oviducts; *R*, rectum. The lizards are oviparous or ovoviviparous.

Intermediate between ovoviviparous and viviparous forms are those in which the young develops for a considerable time in the egg and later becomes attached to the body of the mother. Certain sharks (Fig. 166) exemplify this intermediate condition. In *Mustelus mustelus* the expanded end of the yolk sac becomes attached to the wall of the uterus, forming an organ like the placenta of mammals. The young receive nourishment through it from the mother.

Summary of Locus and Nutrition of Embryo.—The variations in the breeding habits of animals, with respect to the place of development of

FIG. 165.—Uterus of mammal and contained embryo. *F*, fetal placenta; *O*, opening of oviduct; *S*, maternal placenta. (*From Kingsley's Vertebrate Zoölogy, Courtesy of Henry Holt and Company.*)

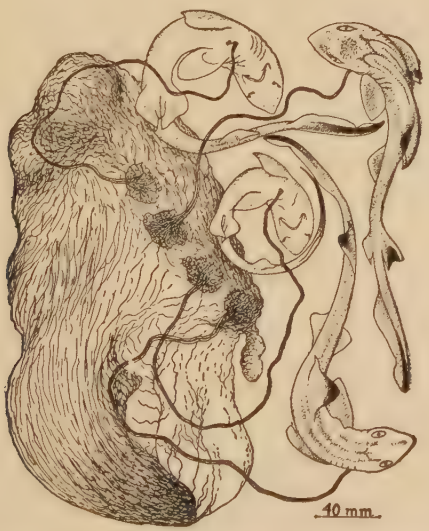

FIG. 166.—Embryo sharks of a viviparous species, *Mustelus mustelus* (Linnæus), attached to the wall of the uterus, which is here dissected open. (*After Fowler.*)

the egg and the source of nutrition of the embryo, may be summarized as follows:

OVIPARITY

(*a*) Eggs fertilized after being laid.

(*b*) Eggs fertilized before being laid.

VIVIPARITY

(*a*) Eggs retained until the young are capable of independent existence as larvæ or adults, but not nourished by the mother. Ovoviviparous species.

(*b*) Eggs retained and the embryo nourished by the mother. True viviparous species.

No Evolutionary Sequence.—It will be seen from the examples given above that just as there is no general evolutionary sequence in the methods of insuring fertilization so there is apparently none in the method of bearing the young. Oviparity and viviparity are found in the vertebrates and the invertebrates. Certain conditions of reproduction itself, however, make one generalization possible. It is to be noted that the forms in which the eggs are fertilized outside the body of the mother are necessarily oviparous. Also, it is only among forms with internal fertilization that viviparity, ovoviviparity and the laying of fertilized eggs can occur. It results that viviparity, ovoviviparity, and the laying of fertilized eggs prevail among land forms, where protection against evaporation of the eggs is necessary, and that the habit of laying eggs before fertilization is mostly found among the aquatic species and the amphibious forms which lay their eggs in water.

Care of Fertilized Eggs.—Among oviparous species the methods of caring for the fertilized eggs are almost endlessly varied in their details. There are many animals which give no care whatever to the eggs. This is particularly true of aquatic species which pour the eggs and spermatozoa freely into the water to come together by chance. The starfishes and sea urchins and many other marine animals exhibit this lack of any parental care. Other forms merely put the eggs in places where development is facilitated. Thus, toads and certain salamanders which live on land in the adult stage lay the eggs in the water. The aquatic turtles come to land to lay the eggs in the warm sand which hastens their development. The digger wasps, ichneumon flies, and certain other insects deposit their eggs in various places and provision them with living or dead animal food. Birds of one group, the Megapodes, lay the eggs in a pile of decaying vegetation, the decomposition of which liberates heat that aids in development (Fig. 167). Again many animals build nests. These nests may be very simple in construction. In the fishes, for example, many species merely hollow out a small area on the botton of the stream by pulling out the pebbles and heaping them up on the downstream side of the nest. The eggs, when laid, drop into this hollow and

among the loose stones. Birds build nests of a great variety of forms, from the loose collection of grass or straw put on the ground by the killdeer, or the insecure litter of twigs set in the branches of trees by the mourning dove, to the elaborate hanging-basket of the orioles. Still other forms enclose their eggs in cases, as was pointed out for the earthworm in the preceding chapter, and as is true also of the leeches and some insects, snails, and spiders.

FIG. 167.—Nest of the Australian brush turkey, consisting of litter in which the eggs are buried to be hatched by the heat of the decomposing vegetable débris. The nest is the heap of débris in the lower half of the photograph. (*Photograph by E. R. Sanborn, loaned by the New York Zoölogical Society.*)

Among the nest-building forms the habit of caring for the eggs has usually been developed, that is, one or both of the parents in many species remain with the eggs until they are hatched. The habit of remaining with the eggs may insure *incubation*, or the elevation of the temperature to a point at which development will proceed. Incubation by the parents is necessary in most birds, and is an aid in some other animals. Remaining with the eggs does not, however, necessarily imply incubation. For example the common skink is a "cold-blooded" animal which remains

with the eggs (Fig. 168). Its temperature is so nearly that of the surrounding air that the development of the eggs can scarcely be affected by the presence of the parent. Some other species apparently incubate the

FIG. 168.—Blue-tailed skink, *Eumeces fasciatus* (Linnæus), with eggs. This lizard buries its eggs (the white mass in the middle foreground) in decaying wood and stays with them until hatched. The curved white streak to the left of the center of the picture is the tail (blue in life) of the parent, and a part of the striped body can be seen to the right of the center. (*Photograph by A. G. Ruthven.*)

FIG. 169.

FIG. 170.

FIG. 169.—*Hyla fuhrmanni* Peracca, a South American tree frog which has the habit of carrying the eggs on the back. The female carries the eggs. (*Photograph by A. G. Ruthven.*)

FIG. 170.—A marsupial frog, *Gastrotheca monticola* Barbour and Noble, from Peru. The opening of the pouch and a protruding egg may be seen in the lumbar region. (*Photograph by G. K. Noble.*)

eggs to a small extent. The python, for example, coils about its eggs, and as the temperature within its coils is a few degrees above that of the surrounding atmosphere, development is thereby probably somewhat

accelerated. The habit of carrying the eggs attached to the body is found in several groups, both among nest-building forms and others that build no nests. Thus, the female crayfish carries her eggs attached to the swimmerets under her abdomen, where she waves them back and forth. The movement of the eggs increases aeration, which is perhaps necessary. Freshwater mussels keep their eggs in the chambers of the gills of the female, where they are furnished oxygen by the water that is constantly passing through the gills. In spiders, the silken egg case mentioned above is often carried about by the mother. Certain frogs (Fig. 169) and insects bear the eggs glued to the back of one sex or the other. In other frogs the eggs are attached to the belly, or the egg masses are wrapped around the hind legs of the male, or are held in the vocal sacs. One frog, the marsupial frog (Fig. 170), has a pouch formed of a fold of the skin on the back in which the eggs are carried. This habit is again found in the pipefish and sea horse (Fig. 171) which carry the eggs in a ventral pouch. Eggs thus carried in pouches may perhaps receive oxygen from the parent, but little is known on this subject. Either the male or female may carry the eggs, but usually only one sex does this in any given species.

FIG. 171.—Hippocampus, the sea horse, male specimen showing brood pouch. *br. ap*, branchial aperture; *brd. p*, brood pouch; *df*, dorsal fin; *op*, opening of brood pouch; *pct. f*, pectoral fin.

Care of the Young after Birth or Hatching: Birth Stages.—After birth in viviparous forms and after hatching in oviparous species the young may or may not require protection and assistance in getting food. This is partly dependent upon the stage of development which the offspring has attained at the time of birth, but not entirely so.

The animal may leave the egg complete in all its parts and needing only the growth of the body and the maturity of the sex cells to attain the climax of its development. Among these forms the young may receive little or no parental care or they may be fed and cared for for many weeks or even months. Among the reptiles, for example, the young are left to their own devices as soon as they hatch or are born. Most fishes and invertebrates also throw off all parental solicitude after their offspring leave the eggs. Most birds, on the contrary, must feed and protect their young for a period of days or weeks; and mammals care for their offspring for weeks or years. In these cases, how long the young must receive aid depends on how far they develop before birth. There are great differences in birth stages even in the same group. Thus among mammals the marsupials (opossums and kangaroos) give birth to young in a very immature state and carry them in a pouch (Fig. 172) until they are well formed; mice are born blind, hairless, and very helpless;

rabbits are born blind but covered with hair; and guinea pigs are born in such an advanced stage that they are very shortly independent of the mother. Among birds are to be distinguished *altricial* and *precocial* forms (Fig. 173), the former usually, although not always, hatched blind and practically without feathers, thus requiring longer parental care, the

FIG. 172.—The black swamp wallaby. The young are born in a very immature stage and are carried in a pouch (marsupium) on the ventral side of the mother. (*Photograph loaned by the New York Zoölogical Society.*)

latter covered with down and with the eyes open, requiring shorter care. The common song birds are all altricial, while domestic fowls, partridges, most wading birds, and the various ducks are precocial.

There are also animals which escape from the egg so early that they lack important organs and must undergo extensive changes to attain the adult form. Or they may possess organs which they must lose before

they become adults. Young animals, leading a separate existence but lacking certain organs of the adult, or possessing organs not found in the adult are known as *larvæ*. The offspring of jellyfishes emerge from the ovary of the mother, where as stated above the eggs are fertilized, as a simple ball of cells, almost at the beginning of development. They receive no care whatever thereafter. The embryos of sponges escape at a stage almost as early as the jellyfishes. The developing embryos of starfishes, sea urchins and their allies (Fig. 174) and marine worms are also capable of free-swimming existence at a very early stage. In the

FIG. 173.—Recently hatched young of the chimney swift, *Chætura pelagica* (Linnæus) (left), and spotted sandpiper, *Actitus macularia* (Linnæus) (right). These are examples, respectively, of altricial and precocial birds.

frogs and toads, the tadpole is a larval form (Fig. 175), but it hatches at a much later developmental stage than do the larvæ of the several preceding examples.

Early development may be direct or indirect. In direct development the embryo develops directly toward the sexually mature condition, the organs being outlined and developed one after the other. In indirect development, on the contrary, organs belonging only to the immature stages and for that reason called *larval organs* are first formed and later destroyed. Thus the caterpillars (larval stage) of butterflies are distinguished from the adult not only by the absence of wings and com-

pound eyes but also by the presence of anal feet and spinning glands which are absent in the adult butterfly; and tadpoles of toads and frogs (Fig. 175) are distinguished from the adult frog not only by the absence of lungs and legs but also by the presence of gills and tail. The transformation by which the larval organs disappear and the missing organs are constructed is known as *metamorphosis*. The more numerous the larval organs the more pronounced the metamorphosis becomes. This phenomenon is further described in Chap. XI.

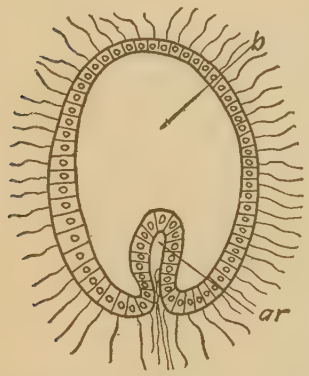

FIG. 174.—Free-swimming larva of the holothurian Synapta, leading an active independent existence at a very early stage of embryonic development. (*From drawing by P. O. Okkelberg.*)

Relation of Birth Stages to Parental Care.—That birth at an early stage of development necessitates parental care would seem at first contemplation to be obvious. That is not usually true, however, except for the animals of common daily observation. It cannot be said for animals as a group that the stage of development at birth determines the amount of parental care necessary, for many of the lower invertebrates with incomplete larvæ and many fishes which have very immature young give no care to the offspring, while other invertebrates with feeble young (for example the ants) carefully guard and feed them. But it is noteworthy that where no care is exercised the young born in early stages are usually those of aquatic or amphibious forms, while the young of terrestrial forms are mostly born in relatively advanced stages or receive parental care. Futhermore, while many aquatic forms give some attention to the young, it is among the terrestrial forms that the greatest development in the habit of caring for the offspring is found. It may thus be concluded that when aquatic animals, or amphibious forms with aquatic young, deposit the eggs or young in suitable habitats they have done much to facilitate postembryonic development; but that land forms must usually give birth to young in an advanced stage of

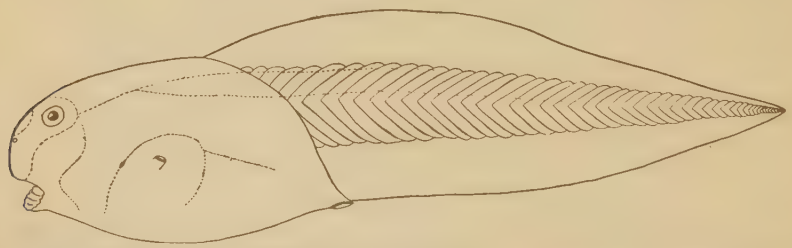

FIG. 175.—Tadpole of frog, illustrating a larval form. Organs are present which are lacking in the adult, and some organs are missing which the adult possesses.

development, or exercise parental care in proportion to the helplessness of the offspring.

Conclusion.—The brief analysis just given shows that the breeding habits of animals are very varied, that they bear some relation to the mode of life, and that there is no general evolutionary sequence in the different methods of copulation, care of eggs, and care of offspring. The habits of disseminating the sexual elements freely into the surrounding medium, of laying unfertilized eggs, and of neglecting the offspring are found most commonly among the aquatic species or species with an aquatic larval period; while the habits of introducing the spermatozoa into the body of the female, the laying of fertilized eggs, ovoviviparity and viviparity, and parental care or the birth of young in advanced stages prevail in terrestrial forms.

CHAPTER XI

EMBRYONIC DEVELOPMENT

Much of the knowledge of the habits by which animals insure the occurrence of reproductive processes and the maintenance of their young during critical periods is comparatively new; but the principal steps by which the fertilized egg is transformed into an animal in the form of the adult have long been known. The field of embryology has been diligently explored, and knowledge of embryonic development is correspondingly definite.

An *embryo*, strictly speaking, is an undeveloped animal while still in the egg membrane, in the case of oviparous or ovoviviparous species, or while attached to the maternal uterus, in viviparous animals. In practice, however, embryology describes more than these stages. In some animals certain organs characteristic of the adult are not yet present at the time of hatching, or the young animal may have organs which the adult does not possess. Such immature animals are spoken of as larvæ. Metamorphosis, described in Chap. X as the transformation of a larva into the adult form, is usually included in embryology. The germ cells, moreover, undergo a characteristic development before they are capable of union in fertilization, and hence before any embryo is produced. This process of development in the germ cells is reckoned as a part of embryology. In the term embryology, therefore, is comprehended the entire development of the germ cells, and of the embryo which they produce, up to the time of birth or hatching, or until such later time as the organs of the adult are laid down and any temporary larval organs are lost.

Early Origin of Somatic Cells.—The differentiation of cells into two general classes, one of which retains the power of reproduction while the other has lost it, is described in Chap. V. It was shown that the distinction between reproductive and sterile cells is found in organisms which are otherwise very simple in structure, such as Pleodorina, while differentiations other than that between reproductive and sterile cells appear only in more complex animals like Hydra. The occurrence of sterile or *somatic* cells, as they are called, in very simple organisms probably indicates that in the evolution of animal forms the distinction between reproductive and somatic cells arose at an early time. In harmony with this view, the somatic cells originate at very early stages in the development of individual animals today. The fertilized egg is in a

sense a germ cell; but development has not proceeded very far until somatic cells are recognizable. These latter and their descendants are incapable of reproduction, and are the beginning of the body. How early the somatic cells arise is accurately known in only a few animals; but it is not improbable that in most animals the same differentiation occurs in a correspondingly early stage. This problem of early differentiation of the somatic and reproductive or *germ* cells is often discussed as the early origin of the germ cells, but from the standpoint of both cytology and evolution it is the somatic cells whose early origin is to be accounted for.

Origin of Somatic Cells in Invertebrates.—The early origin of somatic cells in the embryo has been demonstrated in the arrow worm Sagitta. In the egg of this animal (Fig. 176) is a structure known as the *x-body* which, at the first division of the egg, passes into only one of the two daughter cells. The cell which lacks it is capable of producing only somatic cells, while the one which contains it can, and does, produce

FIG. 176.—Diagram illustrating the early recognition of the somatic and germ cells of the arrow worm Sagitta. At each of the early divisions the x-body (x) passes to only one cell; such cells become germ cells, those that lack the x-body become somatic cells. (*From original diagram by P. O. Okkelberg.*)

both reproductive and somatic cells. When this latter cell divides, the x-body again goes to only one of the daughter cells, the one which lacks it being again capable of producing only somatic cells. At each of the several following divisions the x-body goes to only one of the cells, so that when the embryo has reached the 64-cell stage only one of the cells contains the x-body. The other 63 cells produce only somatic cells. The x-body from that time on, however, divides at cell division so that cells containing it give rise only to germ cells. Whether absence of the x-body from a cell causes it to become sterile need not be debated; but that its absence distinguishes the cell as somatic is certain.

In *Ascaris megalocephala*, a roundworm parasitic in the intestine of the horse, the first exclusively somatic cells are recognizable by the behavior of their chromosomes. When the first two cells derived from the egg divide to form four cells, the chromosomes in one cell remain intact, while in the other the thickened ends of the chromosomes are separated off and cast out into the cytoplasm, and the middle part of the chromosome though retained is fragmented into a number of small pieces (Fig.

177, *A*). The cell with the fragmented chromosomes produces thereafter only somatic cells. In each of the next several divisions the cell with intact chromosomes repeats the process, one daughter cell having fragmented chromosomes, and this latter cell likewise produces only somatic cells. Eventually, however, the one cell with entire chromo-

FIG. 177.—Early cleavage of the egg of Ascaris, showing the origin of the somatic cells. *A*, two-cell stage, with the cells preparing for another division; the chromosomes of one cell remain intact, those in the other cell become fragmented; *B*, the same cells later, showing the ends of the chromosomes in the lower cell being eliminated into the cytoplasm; *C*, the four cells resulting from the preceding division; the lower cells contain masses of eliminated chromatin, and their nuclei are smaller; *D*, division of the preceding four cells, showing a repetition of the fragmentation of the chromosomes in one of the upper cells; *s*, stem cell, from which germ cells are derived; *c*, chromatin eliminated into the cytoplasm in somatic cells. (*From Wilson, after Boveri. Courtesy of The Macmillan Company.*)

somes divides into two cells, each of which has intact chromosomes, and from that time on they give rise only to reproductive cells.

In certain insects the reproductive cells either are larger or contain granules which are lacking in the somatic cells (Fig. 178).

Origin of Somatic Cells in the Vertebrates.—In no vertebrate (backboned) animal has it been possible so far to distinguish somatic cells from germ cells at so early a stage as in Ascaris or Sagitta. However, in

a few vertebrates the difference is visible at a comparatively early embryonic stage, the reproductive cells being lodged among the cells of the lining of the digestive tract. From this position they migrate into the outer layers of the digestive tube, through the mesentery suspending the digestive system from the back, and outward to the place where the reproductive organs subsequently appear. In Fig. 179, which is purely diagrammatic, the reproductive cells are represented as scattered along this path of migration. The earliest stage at which somatic and reproductive cells can be clearly distinguished from one another in vertebrates is thus considerably later than the time of first distinction in some invertebrates. At this stage the somatic cells outnumber the reproductive cells by hundreds or even thousands to one. To the casual observer it is the reproductive cells which attract attention, and as a result one often hears of the origin of the germ cells as a problem of importance. On nearly every theoretical ground, however, it is the origin of the somatic cells that is significant, an idea which is reënforced at the end of the chapter in the discussion of the independence of the germ cells.

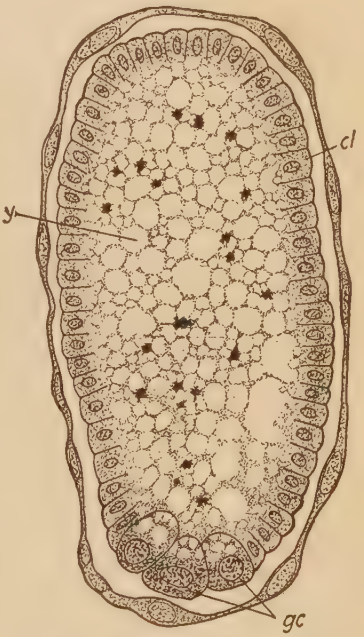

FIG. 178.—Development of the centrolecithal egg of the fly Miastor, showing the cleavage cells (*cl*) at the periphery and the germ cells (*gc*) at the posterior end. (*After Hegner in Journal of Morphology.*)

Maturation.—The germ cells remain for a long time in a relatively undifferentiated condition, showing no signs of the changes which specially prepare them to take part in fertilization and the formation of new individuals. Often it cannot even be stated whether they will become eggs or spermatozoa, yet in most animals, despite their lack of recognition marks, they are irrevocably destined to become the one or the other. During this time they divide frequently by ordinary processes of mitosis, thereby multiplying in number. In this apparently unspecialized condition the reproductive cells are called, in a male animal, *spermatogonia* (singular, *spermatogonium*), in a female, *oögonia.*

Both spermatogonia and oögonia undergo thereafter a series of striking changes comprehended under the term *maturation.* The maturation of germ cells in the male is called *spermatogenesis*, in the female *oögenesis.* In brief, maturation consists of two rapidly succeeding cell divisions, in at least one of which the behavior of the chromosomes is

unlike that which occurs in any other cell divisions anywhere in the body. In these divisions there are many variations in detail in different species, but the fundamental features of the process are the same for nearly all of the higher animals. The account that follows applies to a large number of animals reproducing by the bisexual method.

Spermatogenesis.—This name is given to the maturation of the male germ cells. As soon as the spermatogonia reach the end of their multiplication period, that is, as soon as they have divided by ordinary mitosis for the last time, and are ready to initiate the changes included in maturation, the cells are known as *primary spermatocytes*. The history of

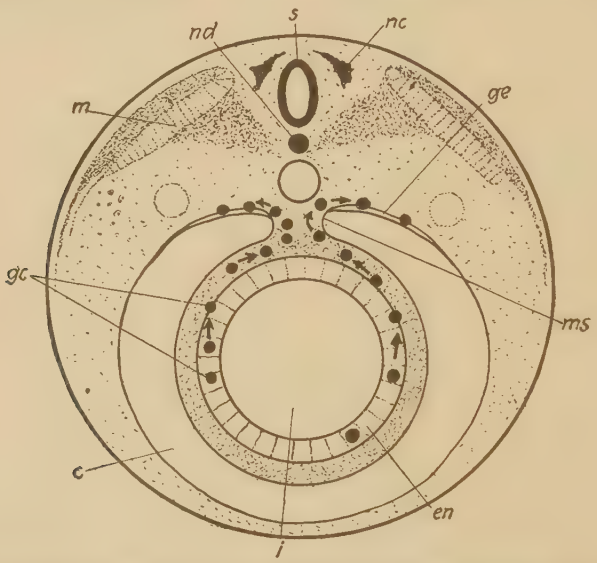

Fig. 179.—Earliest recognition of the distinction between somatic and germ cells in a vertebrate animal. Diagram of cross-section of the body of the embryo, showing germ cells in the endoderm of the intestine and their path of migration (shown by arrows) to the site of the reproductive organs. How much earlier than this stage the somatic cells have lost their reproductive powers is not known. *c*, cœlom; *en*, endoderm of intestine; *gc*, germ cells; *ge*, germinal epithelium which later covers the gonads and from which the germ cells issue; *i*, intestine; *m*, myotome, or muscle segment; *ms*, mesentery; *nc*, neural crest, from which nerves and ganglia develop; *nd*, notochord, forerunner of the backbone; *s*, spinal cord.

these cells in their further development is illustrated in Fig. 180, to which constant reference should be made throughout the following account.

During all of their history up to this time, the germ cells contain the same number of chromosomes as any other cells of the body. That number, barring differences in the sexes, is constant for the species. Now, in an animal descended from two parents, these chromosomes, with certain exceptions that may for the present be ignored, come in equal numbers from the father and the mother. Half of the chromosomes in any cell, whether somatic or immature germ cell, may therefore be designated paternal, the other half maternal. These chromosomes may look pre-

cisely alike, and may in fact be exactly alike; the terms paternal and maternal refer only to their source, not to their nature.

In the early stages of maturation, the spermatocytes grow considerably in volume. In these stages also the chromosomes come together in pairs. Each pair is composed of one paternal and one maternal chromosome. Furthermore, the pairing is not a purely fortuitous occurrence, for each paternal chromosome meets with a particular maternal chromosome. As a result of this union of the chromosomes there are of course half as many pairs as there were chromosomes before.

Tetrads.—The pairs of chromosomes often do not appear as double bodies; for while the chromosomes have been coming together they may also have divided. Each pair thus consists of four half-chromosomes; and the quadruple body formed is called a *tetrad.* Owing to its origin, two of the parts of each tetrad are maternal, the other two paternal. In the two maturation divisions the tetrads are divided, in two planes, first into double bodies called *dyads,* next into their single components.

First Maturation Division.—A spindle is formed, on which the tetrads take their place. How the tetrads are divided depends on the way they are placed on the spindle. In part, this position appears to be fixed and always the same in the same species. In the illustration (Fig. 180), they are represented as having been so placed that the maternal half of the tetrad is separated from the paternal half. It is a matter of chance, however, whether the paternal half is turned toward one end of the spindle or toward the other. It may happen therefore, that all of the paternal dyads go into one cell and all of the maternal dyads into the other, or, as in the figure, part into one cell and part into the other. The cells produced by this division are called *secondary spermatocytes.*

It is worthy of note that in the division just described, no chromosome has divided. The tetrads have divided, but merely by the separation of the two chromosomes which had previously come together. Such a division is called a *reduction division;* it never occurs in cell divisions except in maturation, and in only one of the maturation divisions.

Second Maturation Division.—The secondary spermatocytes divide very shortly by a mitosis in which the dyads are divided into two components. The resulting cells are called *spermatids.* A given spermatid may contain only paternal chromosomes, or only maternal, or both paternal and maternal in any proportion. The number of these chromosomes is only half that of the original spermatogonium.

By a transformation in shape, the spermatid becomes a mature *spermatozoön.* This cell consists usually of a head, which may be rounded or long and slender, and a whip-like tail. The chromosomes are all contained in the head, the tail being merely a motile organ.

Oögenesis.—The maturation of the female germ cells is in most respects similar to that of the male. The early germ cells undergo a period of multiplication in which they divide by ordinary mitosis. During this time they are called *oögonia* (singular, *oögonium*). Eventually this ordinary division ceases, and the cells are ready to initiate the maturation process. At this time they are known as *primary oöcytes*. These

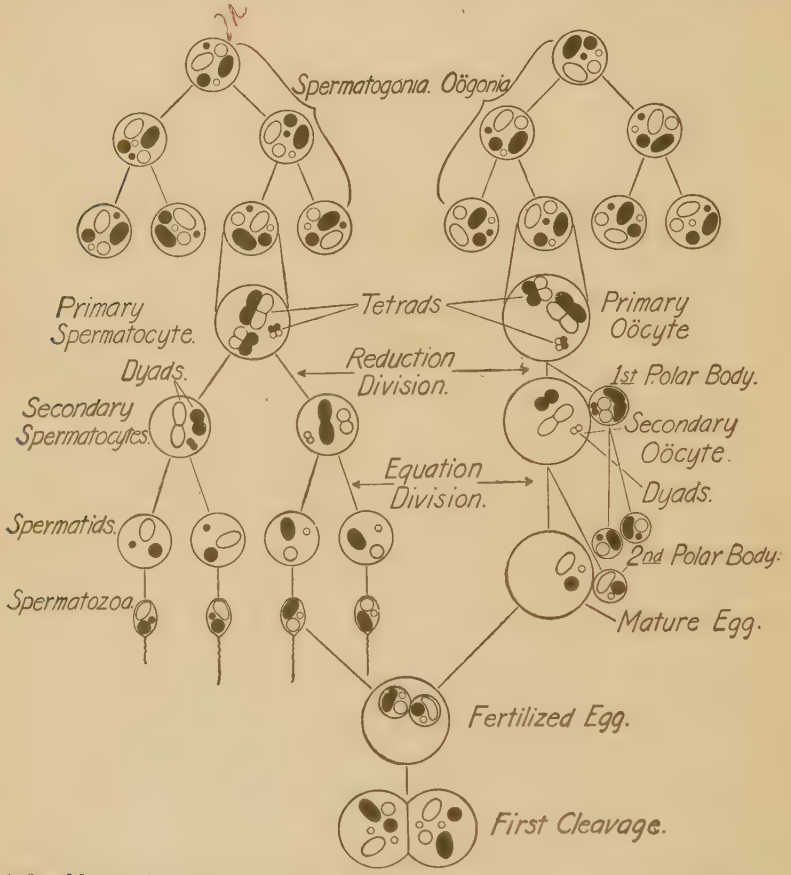

FIG. 180.—Maturation of the germ cells, diagrammatically represented for both sexes. The black chromosomes may be assumed to be of paternal origin, the white ones maternal.

oöcytes grow rapidly to many times their orginal volume, the growth being much greater than in the male.

Tetrads.—During growth the chromosomes meet in pairs, each pair, as in the male, being composed of one maternal and one paternal chromosome. Each chromosome divides as they come together, so that each pair presents a quadruple body, the tetrad. These tetrads are divided in the two maturation divisions, first into dyads, next into their single components, in a manner strictly comparable to the divisions in the male.

First Maturation Division.—When a spindle is formed for the first division, it appears, not in the center, but near the surface; and it is placed approximately perpendicular to the surface. The tetrads take their place on this spindle. If the animal is one in which, as illustrated in Fig. 180, the first division is the reduction division, the tetrads are placed so that the paternal half is toward one end of the spindle, the maternal half toward the other. The resulting cells therefore contain dyads each of which is either wholly paternal or wholly maternal, although of the dyads in a given cell some may be paternal, some maternal. The two cells are of very unequal size, however. One contains nearly all of the protoplasm of the primary oöcyte, the other very little indeed. The disparity between them is much greater than the figure indicates. The larger cell is named the *secondary oöcyte.* The smaller cell is never functional, and is called the *first polar body;* it eventually degenerates.

Second Maturation Division.—In most animals only the secondary oöcyte undergoes further division. In some species the first polar body also divides, and to complete the comparison with maturation in the male this occasional division is represented in Fig. 180, but the resulting two polar bodies are not functional.

The division of the secondary oöcyte involves the division of the dyads into their halves. The division of the cytoplasm is again very unequal, so that one small cell, the *second polar body*, and one large cell are produced. The large cell, unlike the final cells in the maturation of the male, does not undergo any change of shape and hence does not receive any special name; its maturation is finished when the second division is completed, and it is therefore called a *mature egg.*

Comparison of Maturation in Male and Female.—Comparison of the maturation of spermatozoa with that of eggs reveals that with respect to the chromosomes the two processes are parallel. The chromosomes unite in pairs and at the same time divide so as to produce tetrads. Two rapidly succeeding divisions divide the tetrads into dyads and the latter into single chromosomes.

The final cells contain half as many chromosomes as did the germ cell before maturation. These chromosomes may be either paternal, or maternal, or paternal and maternal mixed in any proportion.

The striking feature in which the maturation processes differ in the two sexes concerns the cytoplasm. In the female the divisions are very unequal, so that from each germ cell before maturation there are produced, not four functional cells as in the male, but only one functional cell and two or three degenerate ones.

The Eggs.—When fully formed the germ cells are of various forms in different animals. The eggs are typically spherical or nearly so. Often, however, one diameter is much greater than the others, forming an ellip-

soid. In addition to being elongated, the egg may be curved, as in many insects. Or the widest point may be nearer one end of the egg than the other, as in other insects. The egg is usually polarized, one side being the *animal* pole, the opposite one the *vegetative* pole. The effect of this polarity is referred to below in the account of cleavage.

The size of an egg is closely correlated with the amount of yolk (stored food material) it contains. The eggs of sea urchins and their allies, of the marine worms, the mammals, and others are usually small. Among the oviparous and ovoviviparous vertebrates (reptiles, birds), on the contrary, the eggs are very large. The yolk material is also very differently distributed in the eggs of different species. With respect to the distri-

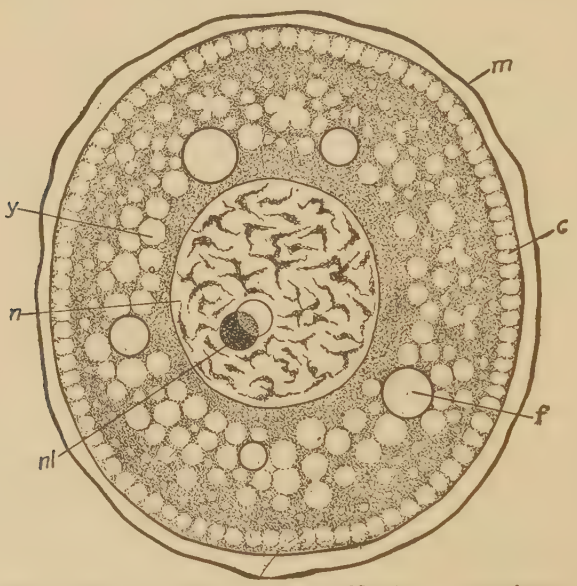

FIG. 181.—Homolecithal egg of the sandworm Nereis. *c*, cytoplasm; *f*, fat droplets; *m*, egg membrane; *n*, nucleus; *nl*, nucleolus; *y*, yolk spheres. (*After Wilson, courtesy of The Macmillan Company.*)

bution of yolk there are recognized three classes of eggs which are of course connected by all gradations. They are as follows:

1. *Homolecithal* eggs are those in which the yolk is nearly uniformly scattered through the cytoplasm. Usually the amount of yolk is not very great. The echinoderms (sea urchins, starfishes), marine worms and mammals produce eggs of this kind (Fig. 181).

2. In *telolecithal* eggs the yolk is massed toward one side, the vegetative pole, leaving the bulk of protoplasm at the opposite side, the animal pole. The yolk is abundant in such cases. The eggs of fishes, reptiles, and birds are strongly telolecithal, while those of the frog are mildly so (Fig. 182).

3. *Centrolecithal* eggs have the yolk occupying the central portion, while the greater part of the cytoplasm is in a layer at the periphery. There is usually also an island of cytoplasm in the middle of the yolk mass, in which the nucleus of the cell is located. Insect eggs are regularly of this type (Fig. 183).

Eggs are very often enclosed in a membrane or shell, particularly among species that lay their eggs on land where evaporation must be largely prevented. These envelopes may be of a chitinous nature, as among insects, or composed of keratin which resembles chitin, or they may be impregnated with calcium salts. The shell of the egg of the domestic fowl is composed of three layers. The inner layer is composed of

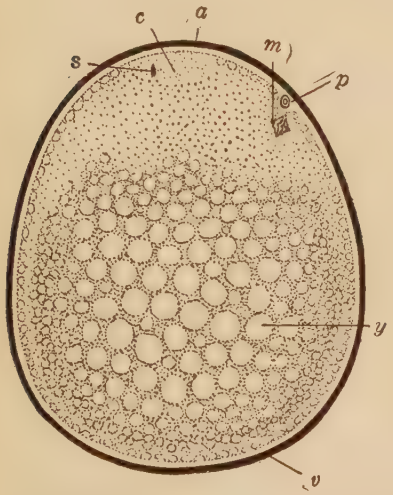

Fig. 182.—Telolecithal egg in generalized form. *a*, animal pole; *c*, cytoplasm; *m*, second maturation spindle; *p*, first polar body; *s*, spermatozoön; *v*, vegetative pole; *y*, yolk crowded toward vegetative pole. (*Modified from original drawing by P. O. Okkelberg.*)

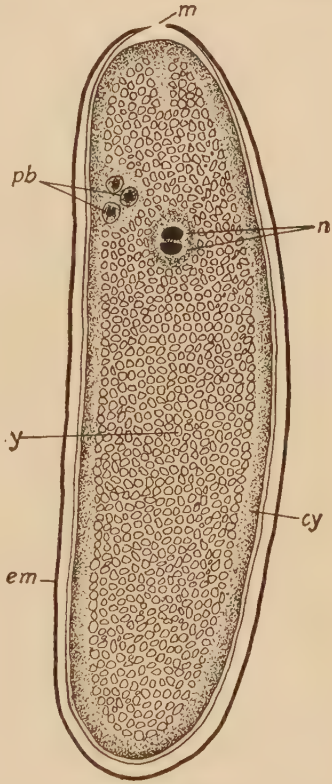

Fig. 183.—Centrolecithal egg of the fly Musca, in longitudinal section. *cy*, cytoplasm; *em*, egg membrane; *m*, micropyle; *n*, egg and spermatozoan nuclei; *pb*, three polar bodies; *y*, yolk. (*From Korschelt and Heider, after Henking and Blockmann, courtesy of The Macmillan Company.*)

calcareous particles with conical faces pointing inward. These particles do not fit closely, and air may pass between them. Outside of this layer is a compact sheet of calcareous strands which also permits the passage of gases. On the outer surface of the shell is a third layer, the cuticle, which appears to be structureless except that it is penetrated by pores. Within the shell is a membrane consisting of two layers of fibers crossing one another in various directions. The envelope as a whole is calculated to

prevent excessive evaporation, a provision necessary in eggs laid in air, and yet it permits the passage of gases necessary for the respiration of the embryo. Indeed, air begins to penetrate the shell soon after the egg is laid, and accumulates in a space between the two layers of the membrane within the shell at the large end of the egg.

The Spermatozoa.—Spermatozoa exhibit much greater variety of form than eggs. Typically they consist of an enlarged anterior *head*, in which the nucleus is contained; a minute body, the *mid-piece*, behind

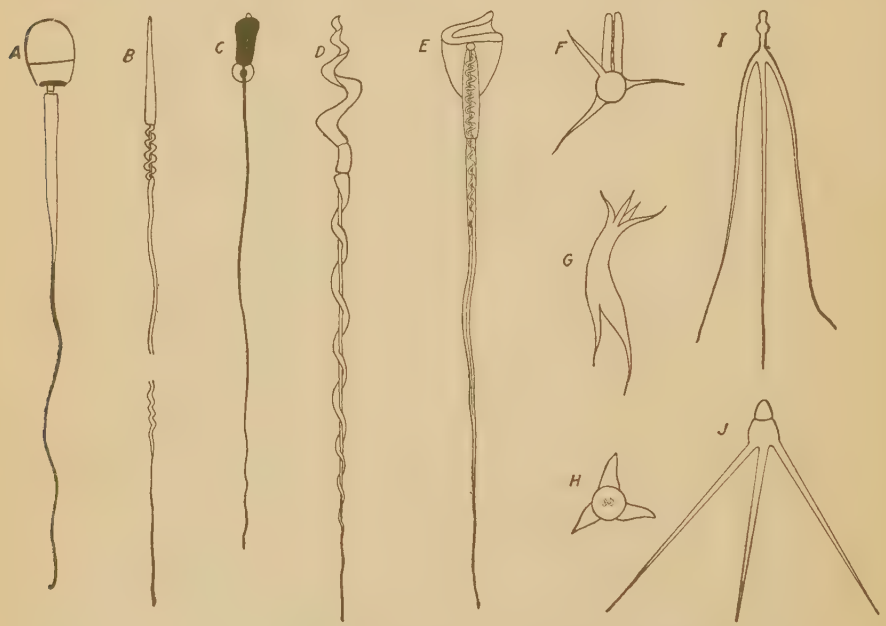

FIG. 184.—Different forms of spermatozoa. *A*, badger; *B*, sheldrake Tadorna; *C*, sturgeon; *D*, flycatcher Muscicapa; *E*, opossum; *F*, lobster; *G*, crustacean Polyphemus; *H*, crab Dromia; *I*, crab Porcellana; *J*, crustacean Ethusa. (*A–D after Ballowitz; F after Herrick; G after Zacharias; H–J after Grobben. From Wilson's The Cell in Development and Heredity, courtesy of The Macmillan Company.*)

the head, from which in some animals a centrosome is known to develop in the fertilized egg; and a whip-like *tail* used as a motile organ. Most of the higher animals produce spermatozoa of this kind, but in a variety of shapes as shown in Fig. 184 (*A–E*). In other animals the form may be wholly different (*F–J*).

Fertilization.—The dual function of the union of egg and spermatozoön has been pointed out in Chap. IX, and some of the methods of insuring that the two cells are brought together are described in Chap. X. It was shown in the latter chapter that the time of fertilization, relative to the location of the egg, is variable; that is, the egg may be fertilized while still in the body of the female, or not until the egg

is laid. In those that are fertilized within the body of the female, fertilization occurs in the oviduct in the vertebrates, or as in some invertebrates while the egg is still in the ovary. It is now possible also to relate the time of fertilization to the stage of maturation which the egg or oöcyte has reached when the spermatozoön enters.

In *Ascaris megalocephala*, parasitic in the horse, the spermatozoön enters the cytoplasm of the oöcyte about the time of the formation of the first maturation spindle. It remains in the oöcyte during the rest of the maturation process. In the frog, rabbit, and some others the spermatozoön enters after the first polar body is formed, but before the second. In the sea urchin the spermatozoön does not enter until the maturation of the egg is complete.

In eggs having a shell at the time of fertilization, there is an opening through which the spermatozoön enters (Fig. 183, *m*). In naked eggs, the spermatozoön may enter anywhere. Usually only one male cell penetrates an egg. Some change, probably of a chemical nature, takes place in the protoplasm of the egg when a spermatozoön unites with it, such that no other spermatozoa can be drawn in. When by accident two or more spermatozoa gain entrance at the same time, abnormalities of development are likely to occur. However, in some animals numerous spermatozoa regularly enter the egg; but the nucleus of only one of them unites with the egg nucleus.

Cleavage.—Shortly after fertilization, within a time measured by minutes or hours in most animals, the fertilized egg begins to divide. This division, which is repeated in rapid succession until the egg is converted into many cells, is called *cleavage* or *segmentation*. In the following account of cleavage the egg may be likened to the earth with its two poles, so that a plane passing through the animal and vegetative poles may be spoken of as *meridional*, other planes as *equatorial* or parallel to the plane of the equator. The manner in which cleavage occurs is related to the distribution of yolk in the egg, so that several types of segmentation are known.

Cleavage in Homolecithal Eggs.—In homolecithal eggs the early cleavage is very regular. The spindle of the first mitosis is horizontal (assuming the animal pole to be above) and near the center of the egg. The first cleavage plane is therefore meridional, passing through both animal and vegetative poles, and dividing the fertilized egg into two approximately equal cells. The sea cucumber Synapta (Fig. 185) is a good example. The second cleavage is also meridional and perpendicular to the first plane; four cells are thereby produced. The third cleavage is nearly equatorial, resulting in eight cells. Often, especially when a distinct amount of yolk is present, the third cleavage plane is slightly above the equator, so that the upper four cells are smaller than the lower quartet.

After the third cleavage there are two or more cleavage planes at the same time. The fourth cleavage passes through two planes, both of them meridional, and perpendicular to one another. The 16 cells thus formed then divide into 32, and so on. Up to the 32-cell stage, in a homolecithal egg, the divisions usually take place at the same time in all the cells. Irregularities occur later, some cells dividing earlier and more rapidly than others. By this cleavage the single cell (fertilized egg) is converted into hundreds of cells forming a nearly spherical mass.

At the point to which the process of cleavage has been followed in the preceding paragraphs, the egg, now more correctly called an embryo, is a hollow ball of cells. Often the cells are arranged in a single layer at the surface, sometimes in a few layers, and there is a cavity in the center filled with liquid. The whole embryo is now designated a *blastula* the cavity within it the *blastocœle*. The blastocœle appears at a very early

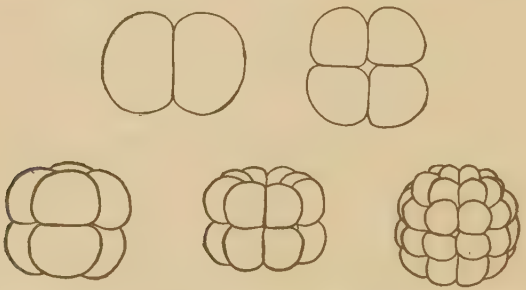

FIG. 185.—Cleavage in the homolecithal egg of the sea cucumber Synapta. The cells are all of nearly the same size. (*Modified from Wilson, after Selenka, courtesy of The Macmillan Company.*)

stage. Even in the four-cell stage, the inner corners of the cells are rounded off, as in Fig. 185, leaving a space. This space is continually present through later cleavages, and becomes larger as segmentation proceeds. The term blastocœle may properly be applied to it in any of these stages.

Cleavage in Telolecithal Eggs.—The extent to which, in the presence of much yolk, cleavage departs from the regular method described for homolecithal eggs, appears to depend on how much yolk is present, and how sharply it is separated from the protoplasm of the egg. In the lamprey, which may be described as "mildly" telolecithal, the egg is divided much as in Synapta, except that the third cleavage plane is far from equatorial (see Fig. 186). The upper quartet of cells in the eight-cell stage is much smaller than the lower. Also, in the lamprey, the irregularities of division occur much earlier and are much more obvious. A blastula is formed, but the blastocœle is eccentric in position (see Fig. 187). The wall of cells is much thicker and is composed of much larger cells at the

vegetative pole than at the animal pole. Cleavage in the frog's egg is very similar to that of the lamprey.

In the eggs of fishes the yolk and protoplasm are almost completely separated; the protoplasm is a convex disc resting on top of the yolk

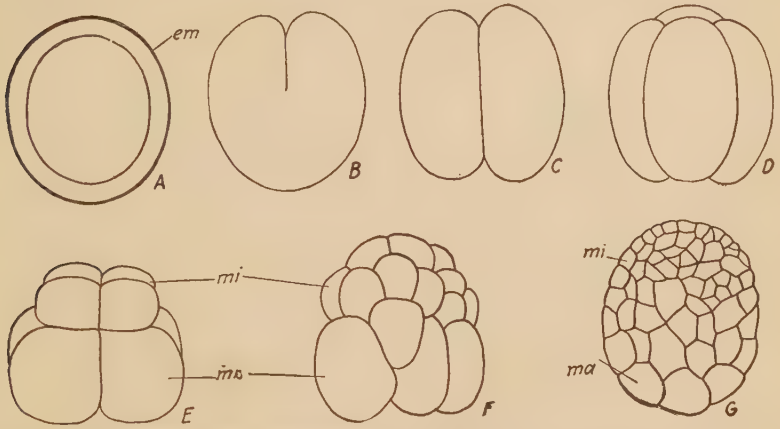

FIG. 186.—Cleavage in the telolecithal egg of the lamprey. The third cleavage (*E*) is distinctly above the equator, and the later cells (*F*, *G*) are very unequal in size. *em*, egg membrane; *ma*, macromeres; *mi*, micromeres. (*Modified from original drawings by P. O. Okkelberg.*)

mass. In such eggs the cleavage is limited to the protoplasmic portion, as shown in Fig. 188. The yolk is never divided at any stage. Cleavage does not follow such a regular scheme as in homolecithal eggs. A blastula is formed, but the blastocœle is only a narrow space between the disc of

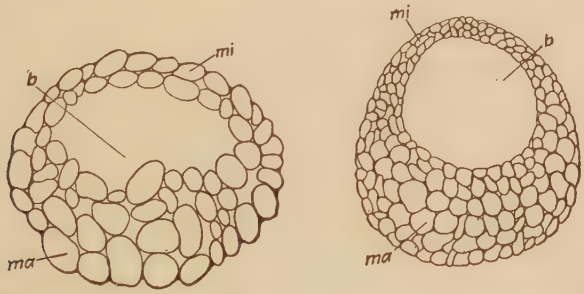

FIG. 187.—Blastula of the lamprey, two stages, in section. The cells are very unequal in size, and the blastocœle is eccentric in position. *b*, blastocœle; *ma*, macromeres; *mi*, micromeres.

cells above and the undivided yolk below (Fig. 189). Scattered cells may, however, rest upon the yolk at the bottom of this cavity.

Like the cleavage of the fish egg is that of the birds and reptiles, whose eggs are also strongly telolecithal.

Cleavage in Centrolecithal Eggs.—Cleavage in the eggs of insects and others of the same type is at first limited to division of the nucleus. The nucleus, ordinarily situated in a small mass of cytoplasm in the middle of the egg, divides repeatedly while the cytoplasm is everywhere unsegmented. The daughter nuclei migrate toward the periphery of the egg, accompanied by small portions of the central mass of cytoplasm, and

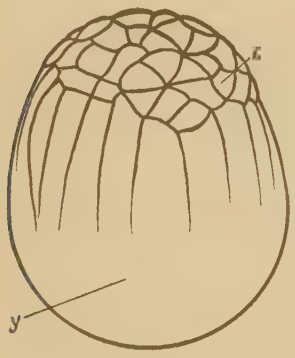

FIG. 188.—Cleavage of the telolecithal egg of the gar pike, *Lepisosteus osseus*, about 5 hrs. after fertilization. The yolk-laden vegetative half of the egg remains undivided. (*After Eycleshymer, courtesy of Gustav Fischer.*)

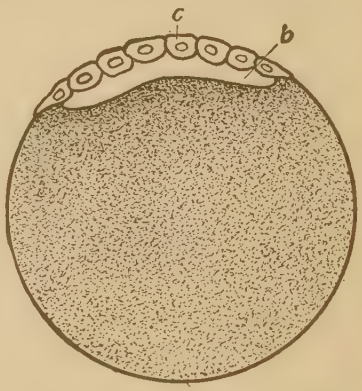

FIG. 189.—Blastula of telolecithal egg, diagrammatically represented in vertical section. *b*, blastocœle; *c*, cleavage cells.

arrange themselves in a layer at the surface. Then division of the cytoplasm takes place between the nuclei (see Fig. 178). For a long time, however, the cytoplasmic divisions do not pass entirely around their respective nuclei, so that the inner ends of the "cells" at the periphery are continous with the mass of the egg.

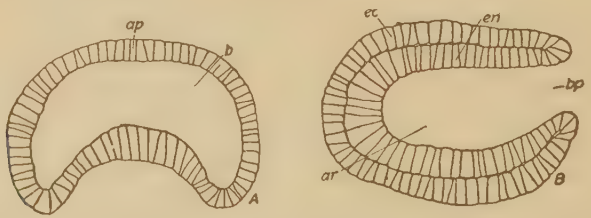

FIG. 190.—Gastrulation in Amphioxus, early (*A*) and late (*B*) stages. *ap*, animal pole; *ar*, archenteron; *b*, blastocœle; *bp*, blastopore; *ec*, ectoderm; *en*, endoderm.

Gastrulation.—When the blastula is well formed it is converted into a two-layered embryo. The process by which this conversion is effected, already briefly outlined in Chap. V, is called *gastrulation*. In different animals it consists of invagination, delamination, or overgrowth, or of a combination of these processes. Some of the simpler methods are described in the following sections.

Gastrulation in Homolecithal Embryos.—The simplest form of invagination takes place in those animals whose eggs have a small amount of yolk evenly distributed. The fish-like Amphioxus and the holothurian Synapta are classical examples (Figs. 190 and 191). The vegetative pole of the blastula becomes flattened, and then turned inward, much as a hollow rubber ball might be indented on one side by pressure. The invagination proceeds until the inturned cells are in contact with those of the opposite side. The blastocœle is thus completely obliterated. The two-layered embryo thus formed is called a *gastrula*. The outer layer of cells, the original animal half, forms the *ectoderm;* the inner layer, the vegetative half of the blastula, is now the *endoderm*. Within the layers of cells is a new cavity, the *archenteron*, which is connected with the outside by a small opening, the *blastopore*.

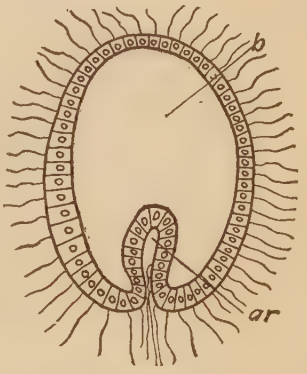

FIG. 191.—Gastrulation in the holothurian Synapta. *ar*, archenteron; *b*, blastocœle. (*From drawing by P. O. Okkelberg.*)

Gastrulation in Telolecithal Embryos.—Blastulas containing much yolk are invaginated in a somewhat different manner. The lamprey (Fig. 192) illustrates the difference very simply. Owing probably to the difficulty of turning in so thick a layer of yolk-laden cells as is present in the vegetative half of the embryo, invagination starts at one side, as in Fig. 192, *A*, approximately half way between the animal and vegetative poles. The inward movement of these cells proceeds until the blastocœle is eliminated, as in homolecithal embryos. Ectoderm and endoderm are thus produced, and an archenteron and blastopore, as illustrated in the figure; but the archenteron is a very much flattened cavity. The endoderm is in part a comparatively thin layer, but in part (the original vegetative part of the egg) a very thick layer.

In blastulas of this type gastrulation is in part accomplished by two processes that are not invagination. The thin layer of cells above the blastocœle, which later becomes in part ectoderm, at first includes only a fraction of the surface of the blastula (see Fig 192, *A*). The ectoderm is extended, during gastrulation, by a process known as *delamination*. As shown in *D*, a layer of cells is split off from the outer part of the original vegetative part of the embryo, thus forming a continuation of the ectoderm.

The other process leading to the formation of the gastrula is one of *overgrowth*. At the lip of the blastopore, where the ectoderm and the thinner part of the endoderm meet, these two layers undergo an active growth, thus creeping down over the vegetative pole of the embryo, as shown at the left in Fig. 192, *C* and *D*.

The end result is a two-layered embryo, the gastrula; but that result is reached by overgrowth and delamination, as well as by invagination.

Gastrulation in the telolecithal embryos of reptiles and birds and in the embryos of mammals is so much modified that these forms cannot be

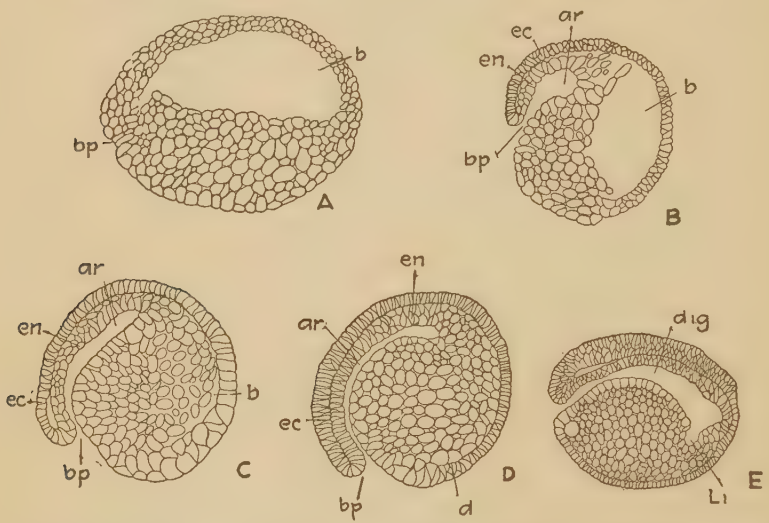

FIG. 192.—Gastrulation in the telolecithal embryo of the lamprey. *A*, *B*, *C*, *D*, *E*, successive stages; *ar*, archenteron; *b*, blastocœle; *bp*, blastopore; *d*, line of delamination; *dig*, digestive tract; *ec*, ectoderm; *en*, endoderm; *Li*, liver. (*After Glaesner, courtesy of Gustav Fischer.*)

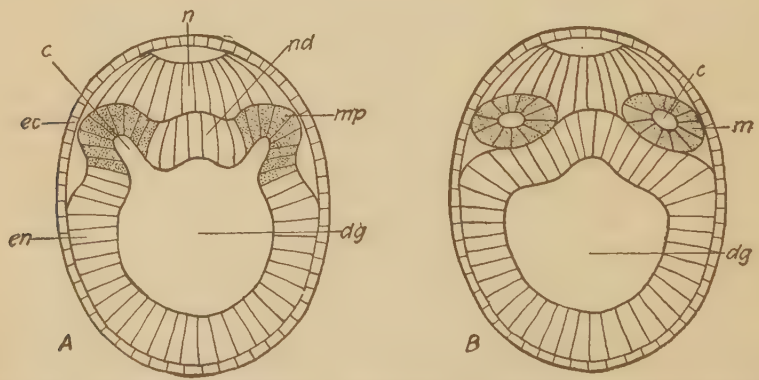

FIG. 193.—Mesoderm formation in Amphioxus. *A*, evagination of the upper lateral portions of the endoderm; *B*, separation of the mesodermal pouches from the endoderm; *c*, cœlom; *dg*, digestive tract; *ec*, ectoderm; *en*, endoderm; *m*, mesoderm; *mp*, mesodermal pouch; *n*, neural tube; *nd*, notochord. (*After Hatschek.*)

here included. Likewise, the early foldings of the layers of cells in developing centrolecithal embryos must be omitted.

Mesoderm Formation.—At the end of gastrulation two layers of cells, ectoderm and endoderm, are present. In all but two groups of metazoa

low in the animal scale, a third layer, the *mesoderm*, is soon formed between these two.

The method of formation of the mesoderm differs in different animals. In Amphioxus the upper portions of the endoderm (Fig. 193) are turned outward in the form of grooves, shown in cross-section in the figure. The edges of each groove meet and fuse, and the groove now in the form of a tube is completely separated from the endoderm. The two tubes thus formed are the mesoderm, and the slender openings in them constitute the body cavity, or *cœlom*. In later stages of development the tubes expand, as in Fig. 194. One side becomes a thin layer of cells applied to the disgestive tract, while the other side lines the inside of the ectoderm.

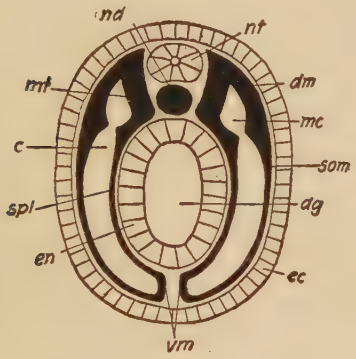

Fig. 194.

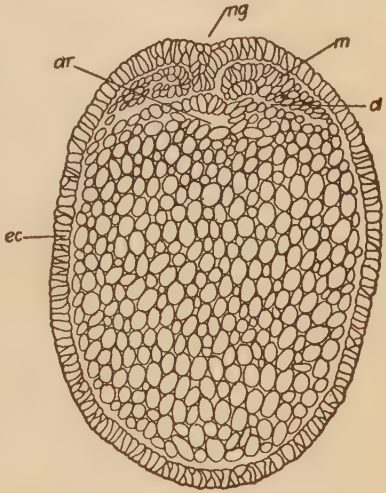

Fig. 195.

Fig. 194.—Cross-section of embryo of Amphioxus, showing expansion of the mesoderm between ectoderm and digestive tract. *c*, cœlom; *dg*, digestive tract; *dm*, dermatome; *ec*, ectoderm; *en*, endoderm; *mc*, myocœle; *mt*, myotome; *nd*, notochord; *nt*, spinal cord; *som*, somatic layer of mesoderm; *spl*, splanchnic layer of mesoderm covering the digestive tract; *vm*, ventral mesentery.

Fig. 195.—Mesoderm formation by delamination in the lamprey. The mesoderm is simply split off the endoderm. *ar*, archenteron; *d*, line of delamination; *ec*, ectoderm; *m*, mesoderm; *ng*, neural groove. (*After Goette, courtesy of Leopold Voss.*)

In telolecithal embryos like that of the frog and the lamprey, the endoderm is so thick that folded grooves like those of Amphioxus could hardly be formed. In such cases the mesoderm may be simply split off from the outside of the endoderm. In Fig. 195, which represents a cross-section of the gastrula of the lamprey, the slit (*d*) above the archenteron represents the beginning of this delamination.

In the higher vertebrates the formation of mesoderm is often a very complicated or obscure process.

ORGANOGENY IN THE VERTEBRATES

The three layers of cells, ectoderm, endoderm, and mesoderm, are often called *germ layers*. They are so designated because certain

organs are derived from each one, so that the layers may be thought of as containing the germs of those organs. If all the facts were known it might be possible to point out the specific cells, even in stages prior to gastrulation, which will become certain organs of the embryo, just as in some animals the somatic and germ cells can be early distinguished. If that were possible, the earliest recognizable cells whose ultimate fate were known would be regarded as the germs of those organs. In the absence of such knowledge, the three layers ectoderm, endoderm, and mesoderm exhibit the first general division of the embryo into parts whose destiny can be predicted—hence the name germ layers.

The development of the organs from these layers is termed *organogeny*. In very large measure the production of organs consists of the rolling, or folding, or protrusion of portions of various layers of cells. When a layer of cells is bent inward, into a cavity enclosed by that layer, the bending is termed *invagination*. If the layer of cells is bent or folded outward, the protrusion is called *evagination*. Invagination and evagination may occur in long and narrow areas, resulting in the formation of furrows or ridges. Or the bending may occur in a very limited region, producing pits or knobs.

Owing to the great diversity of organs found in various groups of animals, and to the fact that many of these organs have no counterpart in other groups, it seems wise to confine the account of the early development of organs to those of the vertebrates. Even within this one group a complete list of organs cannot be mentioned. Some of the more important ones will be described, to illustrate the kind of processes involved in organ formation.

The Early Embryo.—Several of the chief systems of organs are laid down at a very early time. The general arrangement of these systems must be pointed out before any of their parts are traced into later stages. One of the first changes visible externally is the appearance of two prominent ridges, close together, along the dorsal side of the future embryo. These extend lengthwise and are roughly parallel except at the anterior end where they diverge from one another. In a cross-section of the frog, for example, these ridges appear as in Fig. 196. They are the *neural folds*, the beginning of the central nervous system. Where these folds are near one another the spinal cord develops; the divergent folds in front form the brain. These ridges approach one another and fuse along their upper surfaces, cutting off a tube beneath the ectoderm. In longitudinal vertical section at this time, the nervous system appears as in Fig. 197.

Beneath the nervous system a cylindrical rod of cells, the *notochord*, has been separated off from the endoderm beneath. Around it later is formed the backbone.

The digestive tract has been present, as the archenteron, ever since gastrulation took place. At the stage which is described in the preceding

paragraph it is usually enlarged in front and narrowed behind. These parts correspond roughly, in the frog, to the stomach and intestine. Posteriorly the intestine opens to the outside through the *anus* which in

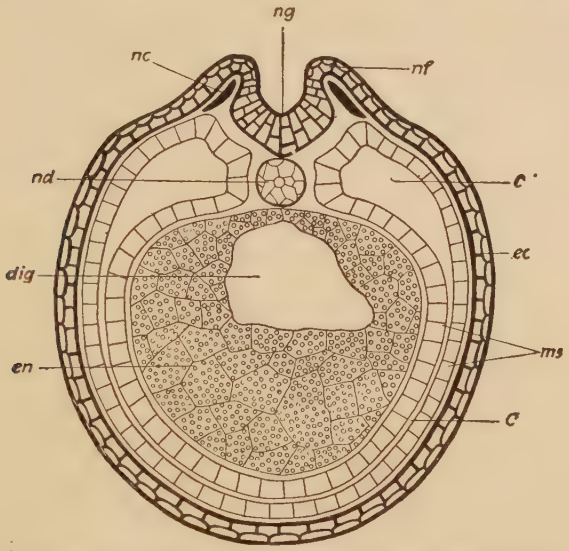

FIG. 196.—Cross-section of the early embryo of a frog, diagrammatic. *c*, cœlom; *dig*, digestive tract; *ec*, ectoderm; *en*, endoderm; *ms*, mesoderm; *nc*, neural crest; *nd*, notochord; *nf*, neural fold; *ng*, neural groove.

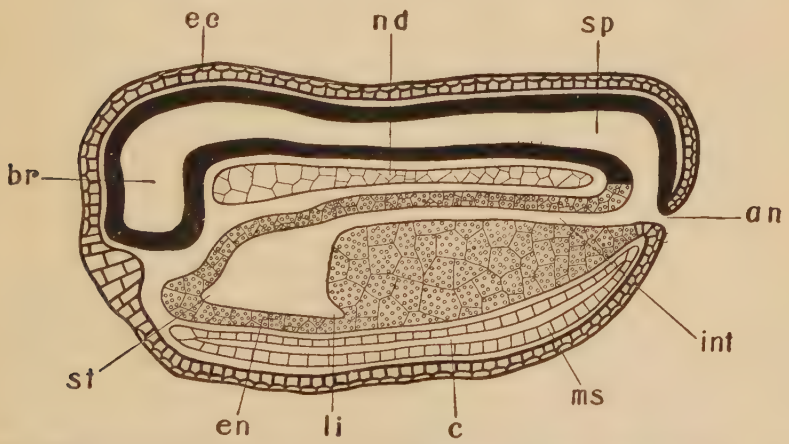

FIG. 197.—Longitudinal section of the early embryo of a frog, diagrammatic. *an*, anus *br*, brain; *c*, cœlom; *ec*, ectoderm; *en*, endoderm; *int*, intestine; *li*, liver; *ms*, mesoderm; *nd*, notochord; *sp*, spinal cord; *st*, stomach.

some animals is the same opening as the blastopore, but in others a passage secondarily produced. In many animals the anus first appears at a much later stage.

As indicated above, and in Fig. 196, the mesoderm is early divided into two layers, one applied to the inside of the ectoderm, the other covering the endoderm. The peritoneum which occupies approximately the corresponding positions in later stages is derived from these layers. Above the endoderm, between it and the notochord, two layers of the mesoderm approach one another and form the mesentery (Fig. 179) which later suspends the digestive tract in a sack of peritoneum. In the longitudinal section (Fig. 197) the mesoderm is not represented above the digestive tract, since the section passes exactly through the median plane. But below the intestine the mesoderm occurs, divided into its two characteristic layers.

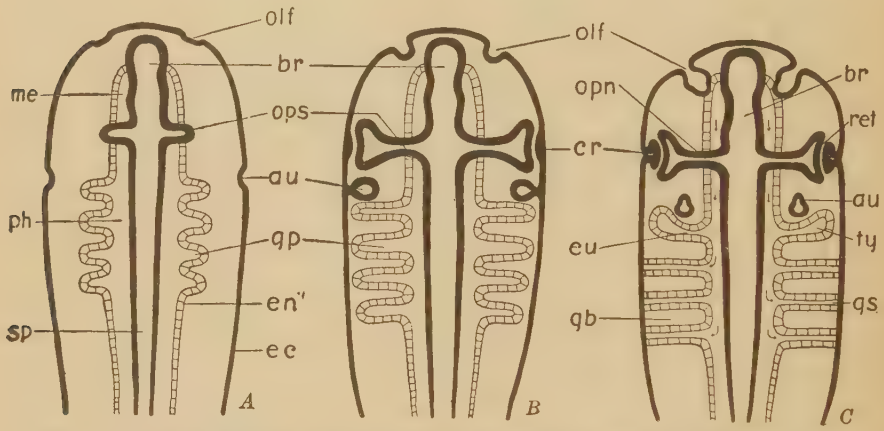

Fig. 198.—Diagrams showing the early development of some of the organs of vertebrate animals, as seen in section from above. The stages here shown are not contemporaneous in all cases. *A*, *B*, *C*, successive stages; *au*, auditory vesicle; *br*, brain; *cr*, crystalline lens; *ec*, ectoderm; *en*, endoderm; *eu*, Eustachian tube; *gb*, gill bar; *gp*, gill pouch; *gs*, gill slit; *me*, endodermal portion of mouth; *olf*, olfactory pit; *opn*, optic nerve; *ops*, optic stalk; *ph*, pharynx; *ret*, retina; *sp*, spinal cord; *ty*, tympanum or middle ear. Arrows in *C* denote current of water through mouth, pharynx, and gill slits.

Digestive Tract and Its Derivatives.—From the invaginated vegetative side of the embryo, which forms the endoderm, is formed most of the lining of the digestive tract, and the lining of organs which branch off from the digestive tract, such as the gill pouches, the liver, lungs, pancreas, and some others.

Gill Pouches.—The *gill pouches*, represented as seen from above in Fig. 198, are evaginations from the sides of the pharynx, or anterior part of the gut. Typically there are five of these protrusions on each side, but some of them are often rudimentary, or two of them may be nearly combined, so that the number frequently appears to be less. Successive stages in the evagination of the gill pouches are shown in Fig. 198, *A*, *B*, *C*. They finally reach the ectoderm, with which they fuse. In fishes

and usually in amphibians the ectoderm and endoderm both break open at the point of fusion, so that the pharynx is open to the outside. These openings are the *gill clefts*. They serve as channels for the passage of water, which enters at the mouth (not shown in the figure since it is at a lower level). The course of the water is indicated in the figure by arrows. In the fishes and in at least the young stages of amphibians gills are developed upon the tissue (*gill bars*) between the gill clefts. The gills are organs for respiration. In the production of certain types of gill the endoderm of the gill pouches has a share.

In the higher vertebrates the gill pouches do not open to the outside at all, or do so only temporarily. They are to be regarded as, to some extent, vestigial organs, an inheritance of an ancestral condition in which functional gills were present. However, some of them are regularly converted during embryonic development into other functional or nonfunctional organs. Thus, the first pouch becomes, as is pointed out below, part of the Eustachian tube and middle ear. Certain of the bars share in the production of the tonsils, the thymus, and the parathyroid glands.

Mouth.—The *mouth* starts as an invagination of the ectoderm from the outside, as in Fig. 199, *m*. For a time it is separated from the rest of the digestive system by a membrane composed of an outer layer of ectoderm and an inner layer of endoderm. This membrane later breaks (Fig. 200), and part of the fore end of the gut is incorporated in the mouth cavity. That part of the mouth derived from the external invagination is of course lined with ectoderm.

Liver.—The *liver* appears at an early stage as an evagination from the lower side of the intestine just behind the stomach. In the frog, the liver is present shortly after the fusion of the neural folds (see Fig. 197, *li*). An early indication of the liver is also shown in Fig. 199, *li*. This pouch grows in extent and soon becomes branched, as in Fig. 200, *li*. One branch at the posterior side of the liver forms the gall bladder (*gb*). The rest are bound together by mesodermal tissue which collects about them, forming part of the body of the liver. The undivided basal portion of the original pouch remains as the *bile duct* (*bd*), through which the secretions of the liver are conveyed into the intestine. During all this development, of course, the liver has been covered by the layer of peritoneum (mesodermal) which invests the entire digestive tract. The adult liver is thus covered by peritoneum, and suspended by mesenteries formed from the same layers of mesoderm.

Pancreas.—The *pancreas* originates from two pouches evaginated from the intestine, as in Fig. 200. One arises from the dorsal side of the intestine nearly opposite the liver (*dp*); the other springs from the angle between the liver and the intestine (*vp*). The latter pouch turns dorsalward, to one side of the intestine, where it unites with the dorsal

rudiment. Their further development which in many respects is similar to that of the liver need not be traced.

Lungs.—The *lungs* take their origin from a protrusion from the ventral side of the gut some distance in front of the stomach, as in Fig. 200, *lg*. This pouch is at first single, as shown in Fig 201, *A*, but soon divides into two parts (*B*, *C*, *D*). As these grow in size they become branched. The undivided stalk of the lung rudiment is the *trachea*, the two principal branches are the *bronchi*, and the finer divisions are the air passages within the lungs. Mesoderm is constantly pushed before the growing lung rudiments, so that the adult lungs are invested with a peritoneum. Other mesodermal tissue is incorporated in the lungs among the air passages, where blood vessels are abundantly developed.

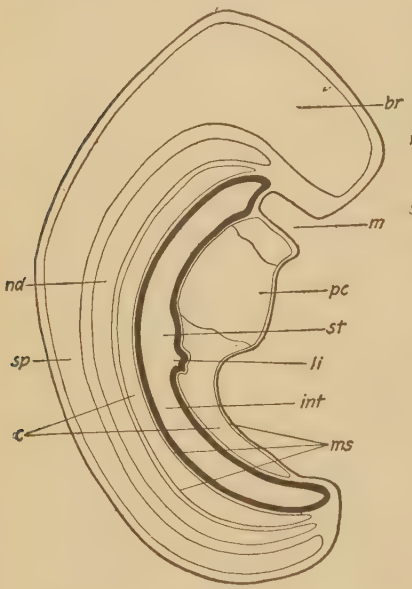

Fig. 199.

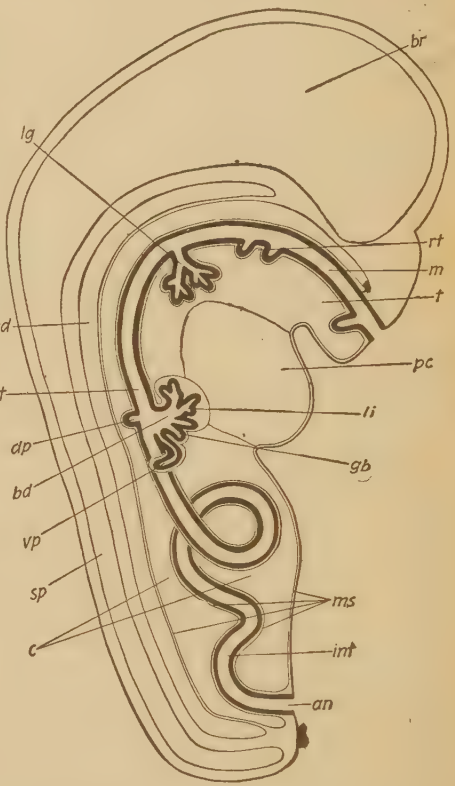

Fig. 200.

Fig. 199.—Diagram illustrating the development of some of the organs of a vertebrate animal as viewed from the side. The section is taken a trifle to one side of the median plane. The stages shown are not all contemporaneous. *br*, brain; *c*, cœlom; *int*, intestine; *li*, liver; *m*, mouth; *ms*, mesoderm; *nd*, notochord; *pc*, pericardial chamber; *sp*, spinal cord; *st*, stomach.

Fig. 200.—Diagram representing the development of some of the organs of vertebrate animals, at a later stage than in Fig. 199. The figure is a trifle to one side of the median plane. The stages shown are not necessarily contemporaneous. *an*, anus; *bd*, bile duct; *br*, brain; *c*, cœlom; *dp*, dorsal rudiment of pancreas; *gb*, gall bladder; *int*, intestine; *lg*, lung; *li*, liver; *m*, mouth; *ms*, mesoderm; *nd*, notochord; *pc*, pericardial chamber; *rt*, root of tongue; *sp*, spinal cord; *st*, stomach; *t*, tongue; *vp*, ventral rudiment of pancreas.

Minor Features of Digestive Tract.—The *tongue* begins in a group of elevations from the floor and sides of the mouth. Two of these elevations are represented in Fig. 200.

The *anus* develops, in a few animals, directly from the blastopore, and in them is never closed. In other animals, in which the blastopore closes by the union of the cells at its margin, the anus opens in another position. The endoderm near the posterior end of the intestine meets the ectoderm, the two layers fuse and then break open. Figure 199 shows the anus as still closed, while in Fig. 200 it is open. The time at which the opening of the anus occurs differs greatly in different forms.

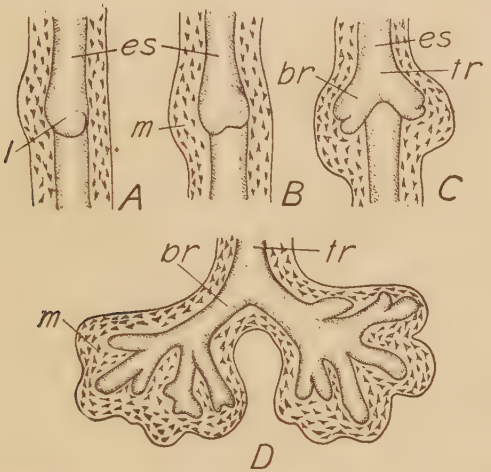

FIG. 201.—Successive stages in the development of the lungs. The esophagus is shown in *A*, *B*, and *C*, but not in *D*. As the lungs grow the mesoderm is pushed before them and thus comes to invest the adult lungs and to make part of the lung tissue. *br*, bronchus; *es*, esophagus; *l*, lung; *m*, mesoderm; *tr*, trachea.

It should be borne in mind that Figs. 199 and 200 are diagrammatic, and do not represent a condition prevailing at any one time in embryonic development. For the sake of compactness, organs have been shown in the same figure in stages which do not occur simultaneously.

Central Nervous System.—It has already been pointed out, and shown in Figs. 196 and 197, that the early central nervous system is a tube formed by the fusion of two folds or ridges of the ectoderm. This tube is wide in the anterior region, where it forms the brain, and narrow posteriorly, where it produces the spinal cord. The thickening and folding of the walls of this tube, especially in the formation of the lobes and cavities of the brain, are too complicated to occupy attention here.

The Nerves.—The nerves extending from the spinal cord take their origin in part from the *neural crests*. These crests are masses of cells budded off from the inner surface of the ectoderm at or near the region

of the neural folds, as indicated in the cross-section of the frog, Fig. 196, and in Fig. 179.

As was pointed out in Chap. VIII, the large nerves arising from the spinal cord are connected with the cord by two roots. The dorsal root is composed of sensory fibers and the ventral root of motor fibers. The dorsal root is enlarged to form a *ganglion.*

This dorsal ganglion is in each nerve developed from one of the neural crests. The dorsal root is completed by processes of nerve cells growing inward from the neural crest and entering the dorsal part of the spinal cord, and by other processes growing outward from the neural crest toward the periphery of the body, forming the sensory part of the spinal nerve. The ventral motor root of the nerve grows out from the ventral part of the spinal cord, and joins the fibers of the dorsal root at a point beyond the ganglion. The nerve fibers from these two roots remain distinct from one another, but are enclosed in the same connective tissue coverings.

The development of some of the cranial nerves (those extending from the brain) is in many respects similar to that of the spinal nerves.

The Eye.—The principal sense organs are developed either as outgrowths from the central nervous system, or as ingrowths, chiefly from the ectoderm, which come secondarily into connection with the nervous system, or by a combination of these two modes of origin. The *eye* begins as an evagination from the side of the brain (Fig. 198, *A*). This protrusion elongates, and at the same time expands at its outer end into a hollow bulb. The bulb-like expansion flattens on its outer side, and is then invaginated to form a double-walled cup resembling a gastrula (Fig. 198, *B* and *C*). The inner layer of this cup becomes the visual part of the *retina* and the basal stalk on which the cup rests is the *optic nerve.* When the outgrowth from the brain comes in contact with the ectoderm, the latter thickens and later invaginates, finally pinching off a rounded mass of cells (*B* and *C*). This mass becomes the *crystalline lens* of the eye. The ectoderm at the point where the lens was formed, becomes transparent, and with additions from the mesoderm in most vertebrates forms the *cornea.* The rest of the eye, including its muscles, is derived from the mesoderm.

The Ear.—The *ear* begins its development in the surface ectoderm, not, as does the eye, from the central nervous system. A patch of ectoderm on each side of the head region thickens, and then invaginates (Fig. 198, *A*), producing a pear-shaped vesicle. The vesicle is pinched off from the ectoderm, and comes to lie within. It changes its shape, producing the characteristic semicircular canals and the (sometimes) coiled body of the inner division of the ear. Only certain groups of cells in this vesicle acquire sensory functions; these groups are joined to the brain by processes of nerve cells growing out from the ganglion of the

eighth (auditory) nerve which, as in the spinal nerves, is derived from one of the neural crests.

The middle ear, which contains the bones of the ear, is derived at least in part from the first gill pouch (Fig 198, *A*, *B*, *C*). In some vertebrates this pouch never perforates to the exterior, in others it opens for a time and then closes again. Its distal end comes beside the vesicle which is derived from the ectoderm, and in this portion the ear bones are much later developed out of mesoderm. The connection of this first pouch with the digestive system either remains open or after closing re-opens again, in either case forming the *Eustachian tube* which connects the middle ear with the pharynx.

The outer ear develops first as an invagination from the outside. The pit or canal thus formed approaches the middle ear, but always remains separated from it by a membrane, the *ear drum*. The shell-like external ears of animals that possess them are erected out of mesoderm with, of course, an ectodermal covering in the epidermis of the skin. The outer ear is not shown in the illustrations (Fig. 198).

Olfactory Organ.—The *olfactory organ*, like the ear, is at first a patch of thickened ectoderm on each side of the head far to the front. This ectoderm invaginates (Fig. 198, *olf*), but unlike the ear the pit thus formed does not close; it remains open to the outside as the *nostril*. The pit enlarges and protrudes inward to meet the front end of the digestive tract just behind the ectodermal part of the mouth. An opening is subsequently formed at this point of contact, and the nostril is thus connected with the deeper portion of the mouth cavity. Only certain parts of the ectoderm that forms the olfactory cavity become sensory. From these parts nerve processes grow toward the brain, thus forming the olfactory nerve. The nasal chamber in many vertebrates becomes curiously altered in form, and receives the ducts of various glands.

The development of the few organs described in the foregoing pages will suffice to illustrate the kinds of processes involved in organogeny, expecially in structures arising from the outer and inner germ layers. Organs and tissues derived from the mesoderm, such as muscles, bones, heart, blood vessels, kidneys and their ducts, are as a rule much less sharply defined in their early stages than are those of the ectoderm and endoderm. A description of their early development is therefore omitted.

Metamorphosis.—Besides the usual course of development, which is in large measure the same for different members of the same group of animals, as described above for a few organs of the vertebrates, some members of a group may undergo an unusual series of changes. *Metamorphosis* is one such series of developmental processes. Animals that metamorphose are born or hatched with one, or several, or many organs which they will not possess as adults, and they may retain these organs for a considerable period after birth or hatching. Or the young animal

may lack organs that will be developed before it becomes adult. The process of losing the larval organs and of gaining the missing adult organs is called metamorphosis.

Metamorphosis in Invertebrates.—Metamorphosis is common among insects, in many groups of which the young stages are wholly unlike the adult. In butterflies, beetles, bees, and flies, the egg hatches into a caterpillar or grub or maggot, from which a person ignorant of the life history could not possibly predict the adult (see Fig. 202). After growth, these larvæ become quiescent *pupæ*, enclosing themselves in a chitinous case and taking no food. They may undergo squirming movements, but

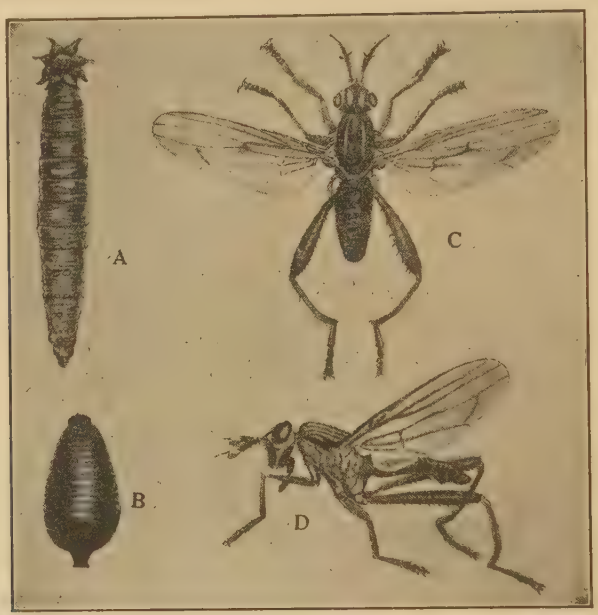

FIG. 202.—Metamorphosis of the swale fly *Sepedon fuscipennis*. *A*, larva; *B*, pupa; *C*, adult from above; *D*, adult, side view. (*From Needham.*)

are incapable of locomotion. In some of them however, remarkable changes are going on in the interior during this quiescent period. Many of the cells of the larva disappear entirely, being dissolved and devoured by certain wandering cells. Whole organs may appear thus to degenerate into a milky pulpy mass. But some cells always remain, and out of these the organs of the adult take their origin. Doubtless the material derived from the degeneration of the lost organs is used as nutrition for the development of the adult organs, but there is much uncertainty as to just what happens during the process. This destruction of the larval organs, and the formation of new organs out of their remains, constitutes for these insects the process of metamorphosis.

Metamorphosis in Vertebrates.—In some of the higher groups, metamorphosis, where it occurs at all, is shrouded in much less mystery. In the vertebrates, the transformation of a tadpole into a frog or toad is the classical example. The readily visible changes are the degeneration of the so-called "sucker," or attaching organ, beneath the head; the development of the legs; and the absorption of the tail, the material of which is probably used elsewhere for growth. Besides these changes are others not so easily followed. The external gills, hidden under a fold of skin called the *operculum*, disappear early, to be replaced by internal gills which are developed on the endodermal lining of the gill slits. The internal gills are lost later, and their function served by lungs, which have all the while been developing. The jaws are provided with a horny armature, serving as teeth, but these are shed and the mouth increases greatly in size. The intestine, from the early tadpole stage a very long and much coiled tube, is greatly shortened. And there are other changes.

Such metamorphoses do not occur in all animals. In many groups, all of the organs that the adult possesses are present in recognizable form at birth or hatching. While these organs may change their relative sizes during postembryonic life, the alterations are so slight that no one would mistake the group to which the new-born animal belongs, even if he were ignorant of its life history. Young birds and mammals (the hairy animals) fall within this category. In such animals there is, of course, no metamorphosis.

MECHANISM OF DEVELOPMENT

The practical identity of the steps of development in all members of the same species of animal creates the problem of the mechanism of this development. What insures that, at a given stage in cleavage, the vegetative half of an embryo shall be invaginated within the animal half? What causes the neural folds to arise always in the same way, and at the same relative time in development? Why does an eye always begin as an evagination at the side of the brain? Why does the vesicle of the inner ear originate behind the eye, instead of in front of it, or in some other location? What causes the protrusion of the endoderm just behind the early stomach, and the subsequent branching of this outgrowth to form a liver?

Explanations.—Most of these changes can be explained as due to inequalities of growth in cells and layers of cells. A layer of ectoderm must bend or fold if at some point one surface of it grows more rapidly than the other. Increase in the size of one cell displaces the cells adjoining it. Actual migration of cells may also be appealed to in the explanation of certain developmental changes.

These explanations are not, however, very far-reaching, for they omit the factors that cause the migration or inequalities in growth of cells. Physiological processes are at the basis of all embryonic development, but the nature of these processes is obscure. It has been suggested that cells react to stimuli, just as organisms react to stimuli. Many animals appear to act in purely mechanical ways in response to changes in their environment, and it is not unlikely that cells of embryos have a similar behavior. The stimuli to which they respond in their growth may be chemical substances diffusing from the cells around them. Or mere pressure of neighboring cells may act as a stimulus to specific kinds of development. It cannot be too strongly emphasized, however, that a statement of the cause of development must be largely conjectural.

Independence of the Germ Cells.—A knowledge of the embryonic development of animals leads to a conception of the relation of the germ cells to the somatic cells that is very useful in the study of genetics and evolution. Although an anatomical examination of the body of one of the metazoa would indicate merely that the *gonad* (ovary or testis) is an organ among a host of other organs, there are reasons for not regarding these organs as being of equal rank. Referring only to the germ cells themselves, and not to the surrounding connective tissue or epithelia whose cells can never have reproductive functions, the gonads must be thought of as occupying a position of superiority. The body is not merely a collection of organs, all of which have come from a common source, the fertilized egg. The fertilized egg is rather a detached representative of the groups of germ cells of the parents, from which a soma (body) has been produced. Viewed in this light, the germ cells are a reserve supply out of which in each generation a soma is erected.

Immortality of Germ Cells.—Germ cells possess a potential immortality. That is, each oögonium or spermatogonium has a chance of producing other germ cells through an indefinite number of cell divisions. There is no necessity of death for any particular germ cell, nor for any specific one of its descendants. It is true, germ cells do die in great numbers. Many eggs are never fertilized, and perish. Gonads always contain some germ cells when the body in which they are located dies, or when the reproductive function of the individual ceases. These remaining cells of course perish. But in each of these cases there is nothing inherent in the germ cells as germ cells which determines that particular cells shall be lost. Each cell has the capacity for escaping from association with its fellows, a chance of uniting with another germ cell in fertilization, an opportunity of giving rise to a new individual in which descendants of the germ cell shall live on and have a chance of surviving. Although some germ cells are inevitably lost, each individual cell has the possibility of avoiding that fate and of being permanent in

the form of germ cells descendent from it. The germ cells are potentially immortal.

Contrasted with the possible permanence of germ cells is the necessary mortality, under natural conditions, of the somatic cells in animals

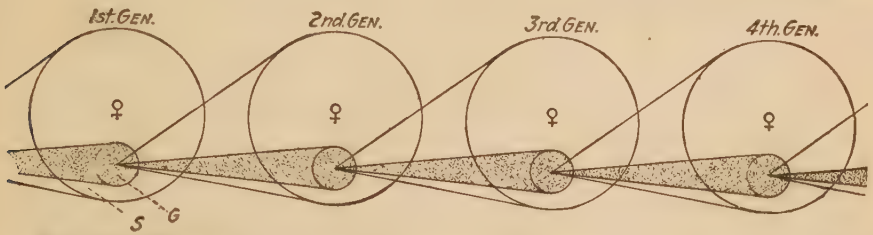

Fig. 203.—Diagram illustrating the conception of the independence of the germ cells in a parthenogenetic animal. The shaded areas (*G*) represent the germ cells, the white areas (*S*) the somatic cells. In each generation germ cells give rise to both germ cells and somatic cells. Somatic cells never give rise to germ cells. Somatic cells can not therefore transmit anything to the germ cells and the next generation merely by descent. (*Modified from drawing by P. O. Okkelberg.*)

reproducing exclusively by the sexual method. No sexually reproducing metazoan body is capable of endless existence. Body cells or their descendants may live on in uninterrupted series for hundreds of

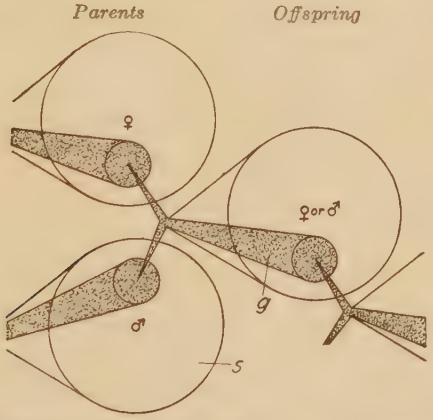

Fig. 204.—Scheme illustrating the conception of the independence of the germ cells in animals reproducing by the bisexual method. The shaded areas (*g*) represent germ cells, the white areas (*s*) somatic cells. In each generation fused germ cells give rise to both somatic cells and germ cells. Somatic cells never give rise to germ cells. Somatic cells therefore can not transmit anything to germ cells and the next generation merely by descent. (*Modified from drawing by P. O. Okkelberg.*)

years in some animals, but they eventually die. No final physiological reason can be assigned for the necessity of death, but experience indicates that there is no escape from it. While the individual is said to have descendants, it is only through the germ cells that these are made possible.

Strictly speaking, it is only the germ cells that have descendants, and the somatic cells of the next generation are some of those descendants.

Germ Cells a Reserve Supply.—The germ cells may in a sense be regarded as being the animal. They constitute a series that may be unbroken for an indefinite time, thus constituting the race. At intervals they may proliferate off from themselves other cells that are temporary, in the form of a body in which the germ cells are lodged. While in this body some of the germ cells escape and form new bodies around themselves. Some germ cells remain in the old body until it is too late to escape; but ordinarily some of them escape before that time, and provide descendants that may live on forever. The germ cells are thus a continuous reserve supply out of which temporary bodies are at intervals developed. This idea is contained in the diagrams in Figs. 203 and 204. The body cells are not, therefore, on a par with the germ cells; for germ cells may and do produce body cells, but except perhaps in very low metazoa it is improbable that body cells ever produce germ cells.[1]

This independence of the germ cells need not be insisted on in most ordinary relations of animals. Indeed, in a physiological sense it may tend to obscure certain fundamental facts, such as the dependence of the germ cells upon the body for nutrition. The body is the enviroment of the germ cells. But in some phases of genetics and evolution the distinctness of germ and body cells is a useful conception.

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[1] Much of the conception of the independence and distinctness of the germ cells and somatic cells is inapplicable to plants, in which germ cells are not formed until late in the life of the individual, and in which germ cells may, under suitable circumstances, originate from many parts of the body.

CHAPTER XII

GENETICS

In the preceding three chapters have been examined the various methods by which new individuals are brought into existence, the habits which insure reproduction and the early care of the young individuals, and the developmental processes which these young individuals undergo in becoming adult. The last of these topics (embryology) was discussed in a general way, with reference only to the major features of animals, those in which not only are all the members of one species alike, but in which members of one large group of animals often closely resemble the members of distantly related groups. Development, however, results in the production of many details in which individuals may differ, but which are just as definitely represented in the fertilized egg as are the nervous system, the digestive tract, or even the gastrula. The production of these minor features and the laws that govern their occurrence are the subject matter of the science of genetics.

Scope of Genetics.—The word genetics means literally the origins of things. Specifically, however, it is applied only to such origins as are implied in heredity, variation, determination of sex, and their applications. Present-day knowledge of heredity was gained through painstaking experiments upon hundreds of animals and plants, and from a study of the cytology of the germ cells and the processes of embryonic development. Out of the facts gleaned from these studies there has come a knowledge of the mechanism by means of which traits are transmitted. A more perfect knowledge of this mechanism is the principal immediate goal of the majority of investigators of heredity, and it is being sought through the medium of experiment and microscopic examination of the structures involved. For the purpose of this chapter, however, the order of discussion may be reversed. The results of breeding experiments will be more readily understood if the mechanism of heredity, so far as it is now known, is described.

The Genes or Factors.—Each inherited character of an animal or plant may be regarded as being produced by a definite something in the undivided germ. This "something" has been given various names, of which *gene* and *factor* are the most commonly used. A fertilized egg contains two genes for each inherited character of the adult that will develop from it; that is, two for color of hair, two for length of stem, two for shape of comb, and so on. These statements would need some quali-

fication in an extended study of heredity, but for the present purpose they are sufficiently accurate. The two genes come from the two parents; one is in the egg before fertilization, the other is introduced by the spermatozoön. They may be like one another, or of different kinds, as is shown later. When the fertilized egg develops into an adult organism, the two genes for each character are handed on through successive cell divisions to the body cells of the adult. Thus every animal produced bisexually has a double hereditary constitution that may be represented by a formula naming the genes which it contains. Theoretically, at least, this formula is the formula of every cell of the body; for the ordinary processes of cell division seem to insure that all the genes contained in the fertilized egg are passed on to every cell produced by that egg.

The mechanism which appears to guarantee that the same group of genes shall be assembled in the daughter cells as was present in the mother cell is found in the equal division of the chromosomes in mitosis. For reasons which will apear as this discussion proceeds, the genes must be regarded as being in the chromosomes. There is strong evidence to show that they are arranged in a row through the length of the chromosome, as shown in Fig. 205. When the chromosome divides in the metaphase of cell division, each gene presumably divides, so that each daughter cell has a chromosome containing the same set of genes as did the parent cell. In animals capable of regenerating missing parts, the general distribution of genes throughout the body may be demonstrated. If the worm Lumbriculus is cut in two, in certain regions, a tail develops from one of the cut surfaces, a head from the other cut surface. Genes for the structures of both head and tail must have resided in the cells at the level of the cut. It is possible, of course, that some unknown feature of cell division may cause the splitting of the chromosomes to be unequal, but the higher animals afford no means of demonstrating such inequalities. By analogy with the lower animals, one would expect genes for eye color to be lodged also in the cells of the liver, and genes for intelligence, in the cells of the leg bones.

The two genes for a given kind of trait occur in two separate chromosomes. One chromosome is maternal, having been in the unfertilized egg; the other is paternal, having been introduced by the spermatozoön. Other genes may reside in the same two chromosomes, but the genes of the one chromosome have to do with the same kinds of characters as do the genes of the other chromosome. Such chromosomes may be said to be homologous with one another. Figure 205 shows a pair of homologous chromosomes, one maternal and one paternal, of the fruit fly Drosophila.

The germ cells, prior to maturation, have the same outfit of chromosomes, and hence of genes, as do the body cells. During maturation, however, their genetic composition is considerably altered. As was

pointed out in Chap. X, homologous maternal and paternal chromosomes meet in pairs during or before the growth period. Then in one of the two maturation divisions (the first in some animals, the second in others), the chromosomes do not split as in ordinary mitosis, but the chromosomes that have come together merely separate again. Each daughter cell receives one of the chromosomes of each pair, not halves

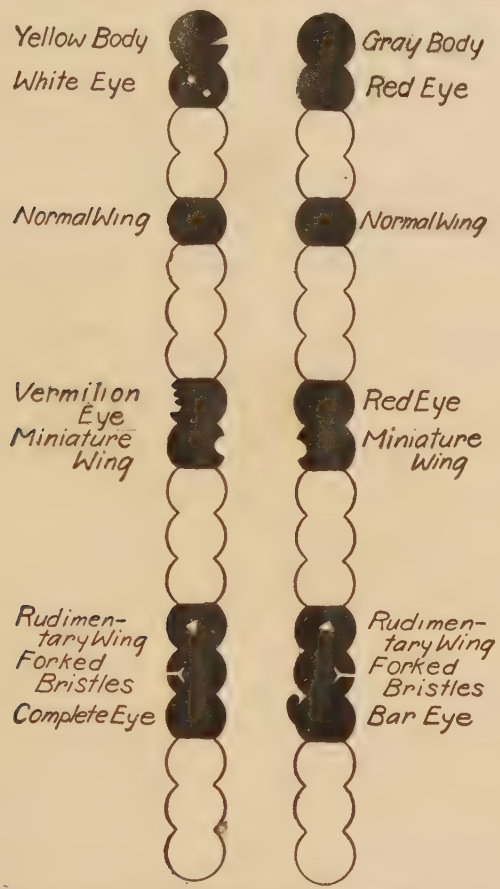

FIG. 205.—Diagrams of two homologous chromosomes of the fruit fly Drosophila. Some of the genes are represented, and are in their proper order through the length of the chromosome. Corresponding genes are located at the same level in the two chromosomes.

of both of them. The number of chromosomes in each daughter cell is thereby reduced to one-half. In the fruit fly Drosophila, while the somatic cells and the oögonia and spermatogonia have eight chromosomes, the mature germ cells have only four.

Moreover, as a result of this reduction division in maturation the germ cells may be different from one another. If the two chromosomes of a pair are precisely alike in all their genes, then all the mature germ

cells will be precisely alike with respect to those genes. If, however, the chromosomes are unlike in some of their genes, the mature germ cells will be unlike. Thus, if an individual contained the two chromosomes represented in Fig. 205, the mature eggs produced by it would all be alike with respect to their genes for size and shape of wings and genes for shape of bristles, but would be of two different kinds with respect to their genes for body color, eye color, and extent of eye. The fact that the different mature germ cells of one and the same animal may carry different genes is of capital importance in heredity.

Terminology.—The hereditary constitution of an animal (with certain exceptions) involves two genes for each kind of character; the hereditary constitution of a germ cell includes but one gene for each kind of character. The formula of an individual is thus a double one, that of the germ cells a single one. The distribution of the genes of a pair to the germ cells is called *segregation*, and it results from the phenomenon of *reduction* (the separation of homologous chromosomes without division) in one of the maturation divisions. Thus, since genes are usually symbolized by letters, if the formula of an animal with respect to any character were AA, the formula of its germ cells would be A. If the formula of an animal were Aa, the genes for one kind of character being unlike, the germ cells would be of two kinds, some with the formula A, others with the formula a. An animal in which the two genes for a given kind of character are alike (AA or aa) is called a *homozygote*, and is said to be *homozygous*. If the two genes of the pair are different (Aa), the animal is a *heterozygote*, or is said to be *heterozygous*. A given animal may be homozygous for some characters, heterozygous for others. A fly containing the chromosomes of Fig. 205 would be homozygous for four characters, heterozygous for four others.

With the foregoing facts concerning the germ cells and their chromosomes in mind, it is possible to analyze the results of breeding experiments. The better known cases rest, as is shown below, upon a very simple foundation.

Color in Guinea Pigs.—Among the well-known animals, the guinea pigs furnish excellent material for the study of heredity. There are many color varieties of these animals, which *breed true;* that is, whenever one member of a pure breed is mated to another like itself, the offspring are all like their parents. Uniformly black animals constitute such a true-breeding variety (Fig. 206). White or albino animals form another such variety (Fig. 207). Albinos are animals in which the usual pigments of the skin, hair, and eyes are wanting, the hair being white, and the skin and the iris of the eye pink. Two such whites mated together always produce white children.

If, now, a black guinea pig of a pure breed is mated with a white guinea pig, the offspring will all be black. Ordinarily the black offspring

are indistinguishable from the black parent. But when these hybrid blacks are mated together, the two original colors reappear. Some of the members of the second hybrid generation are black, others are white. Roughly the blacks constitute three-fourths of the total, the whites one-fourth.

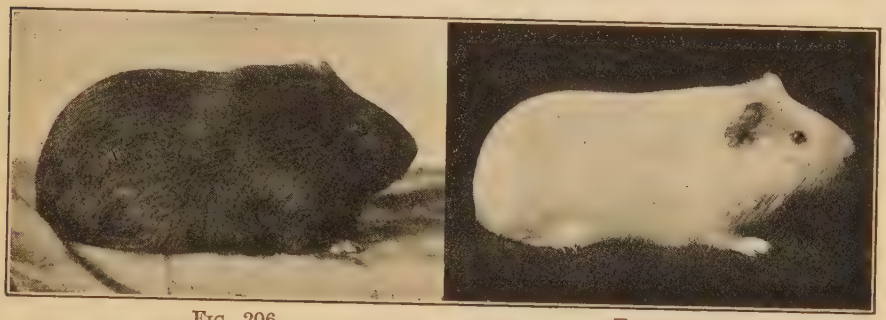

Fig. 206. Fig. 207.

Fig. 206.—A black, smooth-coated guinea pig.
Fig. 207.—A white, smooth-coated guinea pig. (*Both figures by courtesy of Professor W. E. Castle and the Harvard University Press.*)

These results are stated in tabular form in Fig. 208, in which the parents are referred to as P_1, their offspring as F_1 (meaning *first filial* generation), and the second hybrid generation as F_2 (*second filial* generation). Albinism disappears in the F_1 generation, a fact which is expressed by saying that the black coat is *dominant*, or that the white is *recessive*. Its disappearance, however, does not indicate its absence, for albinism reappears in the F_2 generation.

Generation	Nature of individuals
P_1	Black × White
F_1	All black
F_2	¾ Black, ¼ White

Fig. 208.—Diagram showing the results, through two hybrid generations, of mating a pure black and a white guinea pig.

Explanation of the Experimental Results.—The explanation of these results is fairly simple. The genes are in practice designated by letters. When two characters are contrasted, both are commonly designated by the initial letter of the newer character. The dominant character is represented by a capital letter, the recessive character by a small letter. Thus, in the case of color in the guinea pig, when black is contrasted with white, black may be represented by W, white by w, albinism being the more recent character.

The hereditary formulas may now be written for the guinea pigs whose color inheritance was described. The formula of the P_1 black pig was WW, the formula being double because the animal had two parents. In similar manner the formula of the albino parent is to be written ww. When these animals produce germ cells, however, the two genes separate from one another, due to the separation of homologous chromosomes in one of the maturation divisions as explained above, so that each germ cell has only one gene. All the germ cells of the black parent have the formula W, those of the white parent the formula w.

When these germ cells unite in making the cross, the genes W and w are brought together, and the formula of all the F_1 individuals is Ww. One gene W is capable, however, of producing enough black pigment to render the F_1 pigs indistinguishable from the P_1 black. That is the reason for the dominance of black over albinism. If one W could produce only a fraction of the amount of pigment produced by two W's, so that the F_1 pigs were lighter in color than their black parent, the character black would be only partially dominant over white. Cases of partial dominance are not uncommon in other organisms. If one W alone were incapable of producing any pigment at all, all F_1's would then be white, and albinism would be the dominant character, black pigment would be recessive. In that case, also, three-fourths of the F_2 would be white, one-fourth black.

When the F_1 individuals, whose formulas are all Ww, produce germ cells, the phenomenon of segregation occurs just as in the germ cells of their parents. This time, however, since the genes that segregate from one another are unlike, some of the germ cells receive the one gene W others receive the one gene w. The F_1 pigs thus produce two kinds of germ cells, which, if all cells survive, are present in equal numbers. Half the eggs of each female contain W, half contain w. Half the spermatozoa of each male contain W, half contain w. These formulas are shown in the first five lines of the accompanying figure (Fig. 209).

When these two kinds of eggs are fertilized by the two kinds of spermatozoa, there are four combinations, which on the theory of chance should be equally numerous. These four combinations (naming the contribution of the egg first, the spermatozoön second, in each formula) are WW, Ww, wW, and ww. Since, however, in a fertilized egg it is immaterial whether a given gene came from the egg or the spermatozoön, the combinations Ww and wW are identical, so that there are really but three combinations instead of four. This duplicated combination, which is written Ww in Fig. 209, is twice as common as either of the other two. Since one W is capable of producing enough pigment to make a fully black animal, all F_2 animals having the formula WW or Ww are black. Three-fourths of the F_2 generation are therefore black; one-fourth (ww) are white. As pointed out above, however, the F_2 blacks are of two

kinds, practically alike in appearance, but differing in their hereditary behavior. One-third of these blacks are homozygous (*WW*) like the black parent, two-thirds of them are heterozygous (*Ww*) like the F_1 individuals.

The F_3 Generation.—If two individuals of the F_2 generation be mated together, their offspring constitute an F_3 generation. Not all F_3 families

Formulas of parents	*WW*	*ww*
Formulas of germ cells of parents	*W*	*w*
Formula of F_1	*Ww*	
Formulas of eggs of F_1 female	*W* and *w*	
Formulas of spermatozoa of F_1 male	*W* and *w*	
Formulas of F_2	¼ *WW*, ½ *Ww*, ¼ *ww*	

FIG. 209.—Diagram showing the genetic formulas of all individuals and their germ cells, as far as the F_2 generation, involved in the cross between a homozygous black and a white guinea pig.

are alike, however, for there are three kinds of F_2 individuals from which to select parents. Thus there are six possible matings between F_2 individuals. With the results of four of these we have already become familiar in the matings previously described. For example, one might mate two F_2 individuals each of which was of the composition *WW*; in this case, of course, all the F_3 individuals would be homozygous blacks.

Formulas of parents (F_2)	*Ww*	*ww*
Formulas of germ cells of black F_2 parent	*W* and *w*	
Formula of germ cells of white F_2 parent	*w*	
Formulas of F_3 individuals	½ *Ww*	½ *ww*

FIG. 210.—Diagram showing the result of mating a heterozygous black guinea pig with a white animal. This result is one of the possibilities in the production of an F_3 generation.

Or the two F_2 parents might both have the formula *ww*, in which case the F_3 offspring would all be albinos. Or one of the F_2 parents might be homozygous black (*WW*), the other white (*ww*); in this case the F_3 generation would be all black, but heterozygous (*Ww*), just like the F_1 generation of Fig. 209. Or the F_2 parents might both be *Ww*, so that the F_3 generation would be of three kinds, just like the F_2 generation in Fig. 209.

The other two possible matings between F_2 individuals are $Ww \times ww$, and $WW \times Ww$. Crosses of these two types are often made between F_1 animals and their two parent varieties, and are then spoken of as *back crosses*. The results of the former cross, that of a heterozygous black with a white, are shown in Fig. 210. The first formula in F_3 is of course that of a heterozygous black, the second that of a white animal.

The other remaining possible mating in F_2 for the production of an F_3 generation is that between a homozygous black (WW) and a heterozygous black (Ww). The nature of the F_3 in such a case may be determined from Fig. 211. All of the F_3 animals in that diagram are black, but half of them are homozygous, half of them are heterozygous.

It is not necessary to carry this account beyond the F_3 generation. The nature of the F_4 and succeeding generations would depend on principles illustrated in the production of the F_3. No new matings are possible.

Formulas of parents (F_2)	WW	Ww
Formula of germ cells of homozygous black parent	W	
Formulas of germ cells of heterozygous black parent	W and w	
Formulas of F_3 individuals	$\frac{1}{2}WW$	$\frac{1}{2}Ww$

FIG. 211.—Diagram showing the result of mating a homozygous black and a heterozygous black guinea pig. This result is one of the possibilities in the production of an F_3 generation.

The actual results described in this account are not in themselves important. But it is important that the student should be able, in the case of any two parents whose hereditary formulas for a single character are known, to predict the nature and formulas of all of their progeny. Thorough familiarity with the principles involved in the guinea pig matings described above should insure this ability.

Accuracy of the Ratios.—In describing the offspring of various matings it has seemed advisable to start from the formulas in many cases and state the result that is expected on theoretical grounds. When an F_2 was described as being composed of 75 per cent of black individuals and 25 per cent whites, no particular experiment was in mind. The proportion stated is the one theoretically expected. In a large number of individuals, if there are no disturbing circumstances, such as a greater death rate in one of the classes than in the other, the actual observed numbers are rather close to the theoretical ones. One actual experiment which should theoretically have resulted in an F_2 of two classes, of 75 per cent and 25 per cent respectively, did actually result in 72 per cent and 28 per cent respectively. How nearly observed results approach the theoretical may be determined by the student, without the labor of a

breeding experiment, by tossing pennies. If two coins of regular form, with edges perpendicular to the flat surfaces and with sharp corners, be tossed upon a hard smooth surface, heads and tails should turn up in the following proportions: in one-fourth of the throws both heads, in one-fourth both tails, in one-half one head and one tail. The mathematician can compute how far observed results may diverge from the theoretical without indicating any defect in the theory, but for most persons the trial by pennies is more convincing.

Simultaneous Inheritance of Two Independent Pairs of Characters.— In many cases it is important to trace the inheritance of two pairs of contrasted characters at the same time. This is not a needless complication of what is otherwise a simple matter, for some of the most important advances in our knowledge of heredity have followed from such simultaneous tests. An example in guinea pigs will make clear the usual relation between two independent pairs of characters.

In most guinea pigs the hair on the back all slopes in one general direction, producing a smooth coat. The animals in Figs. 206 and 207 both have smooth coats. In some, however, the hair is arranged in whorls, sloping away from a central point in each whorl. The occurrence of several such whorls on the back gives an animal a very unkempt appearance, and it is said to have a rough coat (Fig. 212). Rough coat is found to be dominant over smooth, and all of the numerical results obtained with black and white animals in F_2 and F_3, can readily be duplicated with rough and smooth coat.

When these two pairs of characters are studied in the same animals, they behave independently of one another. If a smooth black pig, homozygous for both these characters, be mated with a homozygous rough white animal, all the offspring will be black and rough (see Fig. 213, F_1). The one dominant character is contributed by the one parent, the other dominant character by the other parent. If, now, the F_1 black rough animals are mated together, the F_2 includes all the possible combinations of the two characters; some animals are black rough, some black smooth, some white rough, some white smooth, as indicated in Fig. 213. These combinations are not equally numerous, however. Of every 16 F_2 individuals, in the long run, 9 have both dominant characters (black rough), 3 have the one dominant (black smooth), 3 have the other dominant (white rough), and one has both recessives (white smooth). The results may be understood in part from Fig. 214 which, if the account of the inheritance of a single pair of characters has been mastered, will require no further explanation.

The last line in Fig. 214 may need explanation. In the segregation of the genes at the time of maturation, in F_1 pigs, W segregates from w entirely independently of the segregation of R from r. Thus W may happen to go into the same germ cell with R or with r. In like manner

FIG. 212.—Two guinea pigs with rough coats. The hairs are in many places arranged in whorls, sloping away from the central point. Rough coat is dominant over the smooth coat of Figs. 206 and 207. (*Courtesy of Professor W. E. Castle and the Harvard University Press.*)

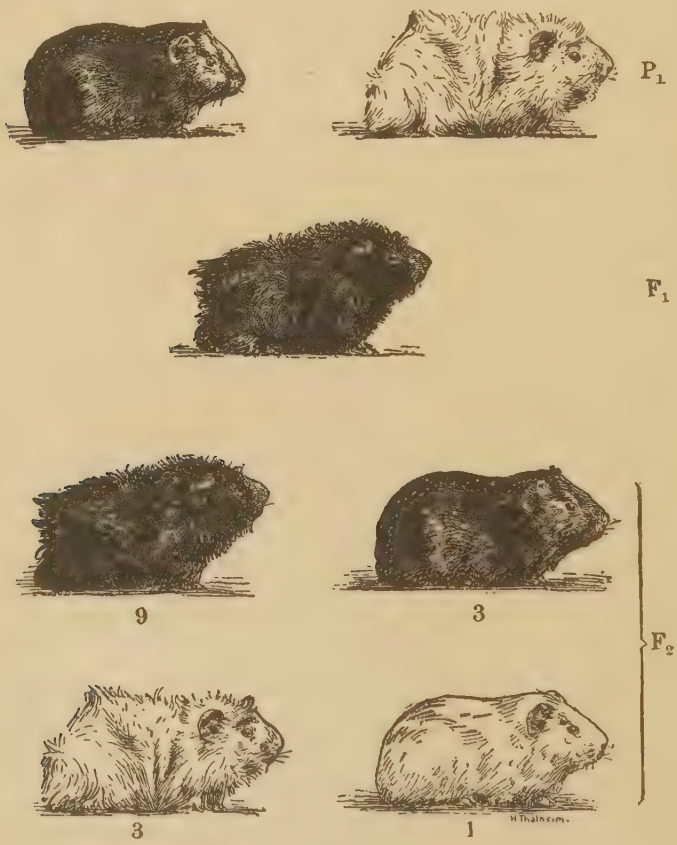

FIG. 213.—Illustration of the simultaneous inheritance of two pairs of independent characters. The parents are black smooth, and white rough, respectively. Black and rough are dominant. The F_2 generation consists of four visibly different types, in the ratio of 9 black rough: 3 black smooth: 3 white rough: 1 white smooth. (*From Babcock and Clausen, after Baur.*)

w may be carried into the same germ cell with *R*, or with *r*. Theoretically, in the case of wholly independent characters such as these two, the four combinations *WR*, *Wr*, *wR*, and *wr* should occur with equal frequency. Of the eggs produced by an F_1 female (*WwRr*) in the above case, 25 per cent should possess each of the combinations named in the last line

Visible characters of parents	Black smooth	White rough
Formulas of parents	*WWrr*	*wwRR*
Formulas of germ cells of parents	*Wr*	*wR*
Formulas of F_1 individuals	*WwRr*	
Formulas of germ cells of F_1	*WR*, *Wr*, *wR*, *wr*	

FIG. 214.—Diagram showing the formulas of the individuals and germ cells involved in a cross between a black, smooth-coated guinea pig and a white, rough-coated animal. The F_2 animals are not represented.

of Fig. 214. In like manner, the F_1 males should produce spermatozoa of the same four hereditary compositions, 25 per cent of the spermatozoa being of each kind.

When the four kinds of eggs are fertilized by spermatozoa, any kind of egg may be fertilized by any kind of spermatozoön. *Wr* (egg) may combine with *wr* (spermatozoön), or with *WR*, or *Wr*, or *wR*. Theoretically these combinations should occur with equal frequency. Each kind of egg may be fertilized by any one of the four kinds of spermatozoa. Sixteen combinations are thus possible. For the practice of beginners, these combinations may well be written in the form of a checkerboard, in the following manner. Write each egg formula four times in a *horizontal* row, at some distance apart. Then write each spermatozoön formula four times in a *vertical* row, placing the formula of the spermatozoön under the formula of the egg. The result is shown in Fig. 215.

The four letters in each group are the hereditary formula of one kind of F_2 animal. Whenever at least one *W* and at least one *R* are included in this formula, the animal is black and rough. There are nine of these out of each sixteen. When at least one *W* is present, with two *r*'s (hence no *R*), the animal is black and smooth. There are three of these in each sixteen. When at least one *R* is present, with two *w*'s (hence no *W*), the animal is white and rough. There are three of these in each sixteen. When neither *W* nor *R* is included in the formula (that is, when two *w*'s and two *r*'s are present), the animal is white and smooth. There is one such animal in each sixteen. The ratio 9:3:3:1 is the characteristic ratio in F_2, when two independent pairs of characters are studied simultaneously. While this ratio, and the proportions stated above, are given with mathematical precision, it is nowhere intended to imply that every

sixteen animals will be divided exactly this way. One class might easily be wanting entirely in so small a number. Actual results of breeding experiments, however, accord as nearly with the expected proportions as the laws of chance require.

Egg of F_1	*WR*	*WR*	*WR*	*WR*
Spermatozoön of F_1	*WR*	*Wr*	*wR*	*wr*
Nature of F_2	Black, rough	Black, rough	Black, rough	Black, rough
Egg of F_1	*Wr*	*Wr*	*Wr*	*Wr*
Spermatozoön of F_1	*WR*	*Wr*	*wR*	*wr*
Nature of F_2	Black, rough	Black, smooth	Black, rough	Black, smooth
Egg of F_1	*wR*	*wR*	*wR*	*wR*
Spermatozoön of F_1	*WR*	*Wr*	*wR*	*wr*
Nature of F_2	Black, rough	Black, rough	White, rough	White, rough
Egg of F_1	*wr*	*wr*	*wr*	*wr*
Spermatozoön of F_1	*WR*	*Wr*	*wR*	*wr*
Nature of F_2	Black, rough	Black, smooth	White, rough	White, smooth

FIG. 215.—Diagram showing the sixteen possible combinations of F_1 eggs and spermatozoa, hence the sixteen possible kinds of F_2 individuals, in crosses where two independent pairs of characters are involved.

Interaction of Genes.—Sometimes when two genes of different pairs are present in the same individual, they work together to produce a result unlike that of either one alone and unlike any obvious combination of their separate visible characters. An example is found in the combs of fowls. Pea combs and rose combs, shown in Fig. 216, are definitely and separately inherited. Each one is dominant over single comb, and when either one is crossed with single comb all the numerical results characteristic of a simple cross like that between guinea pigs of different colors described on pages 216–220 are obtained. When, however, pea-combed and rose-combed fowls are crossed, their offspring have combs in the form of an irregularly rounded lump known as the walnut comb. When these F_1 walnut fowls are bred together, the genes for pea and rose combs are independently distributed, and sixteen combinations are produced in F_2, just as in Fig. 215. Of these F_2 combinations, it need only be pointed out that the nine-sixteenths which possess factors for both pea and rose combs will have walnut combs. The remaining members will have pea, or rose, or single combs. The interaction of factors of different pairs is common; probably it is universal. It is one of the difficulties that lie in the way of rapid discovery of the facts of heredity in many animals.

Gregor Mendel.—The simple operations of heredity described in the foregoing paragraphs are in accordance with what is known as Mendel's Law. An Augustinian monk, Gregor Mendel (Fig. 217), who labored

in the monastery at Brünn, in Austria, in the latter half of the last century, found time to experiment with garden peas on the monastery grounds. He knew a number of varieties which differed from one another in the height of their stems, the form and color of the seeds, the shape and color of the pods, and the position of the flowers. From crosses between these varieties Mendel derived the simple law of heredity which bears his name. He published the results of his experiments in 1865 and 1866, but they attracted no attention. Probably because biologists were engrossed with Darwin's theory of Natural Selection, which had been announced a few years before, Mendel's work lay unnoticed for a third of a century. Then, in 1900, three European biologists, working independ-

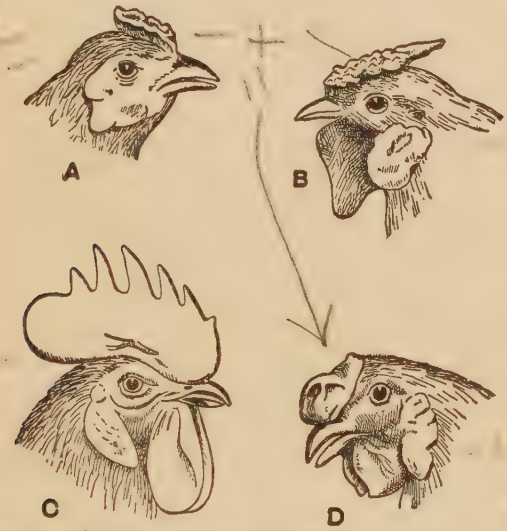

FIG. 216.—Walnut comb (*D*), a character produced by the interaction of genes for pea comb (*A*) and rose comb (*B*). Single comb (*C*) is produced when neither the gene for pea comb nor that for rose comb is present. (*From Punnett, Mendelism, courtesy of The Macmillan Company.*)

ently, rediscovered the principle which Mendel had published. At the same time Mendel's paper was brought to light, and his three successors in this field generously gave him the credit that was his due. Since 1900 Mendel's Law has been abundantly verified. Although his scheme of inheritance has been elaborated since that time, the fundamental features of it are now generally recognized as applicable to the bulk of the known facts regarding heredity.

Mendel's Law.—The fundamental features of Mendelian heredity are the segregation of the genes in the production of the germ cells and their independent distribution to the germ cells. The two genes concerned with a given character separate from one another, going to different germ cells. Different pairs of genes segregate, in most instances,

independently of each other, so that genes may be brought together in the germ cells in combinations that never existed before. As a result, the inherited characters of animals may be grouped in ever new combinations. Because such inherited traits as color of hair, color of eye, length of ear, length of hair, and direction of hair can be combined in new ways in hybrid individuals, they have sometimes been called *unit characters*. That these characters behave as units is due to the segregation and independent assortment, resulting in new combinations, of genes in the germ cells. These are the essential features of Mendel's Law. That law does not require dominance, for there are cases in which

FIG. 217.– Gregor Johann Mendel, 1822–1884, to whom is due much of the present activity in the study of genetics. (*Reproduced from the report of the Royal Horticultural Society Conference on Genetics*, 1906. *By permission of the President and Council.*)

dominance is lacking but all other phenomena are typical. No particular ratios, such as 3:1, are necessary, since many things may conspire to alter these ratios. Mendel's Law refers to the segregation and independent assortment of the genes.

Linkage.—That part of Mendel's Law calling for independent assortment of the genes of different pairs is not always valid. Different pairs of genes are independent only when they are in different pairs of chromosomes. When two genes are in the same chromosome, they remain together more often than not in the distribution of the factors to the germ cells.

A concrete example is that of black color of the fruit fly Drosophila (contrasted with the normal gray color) and vestigial wing (contrasted with the normal long wing). These characters are readily recognizable in Fig. 218. If a gray vestigial fly is crossed with a black long-winged fly, the offspring are gray and long-winged. The composition of the F_1

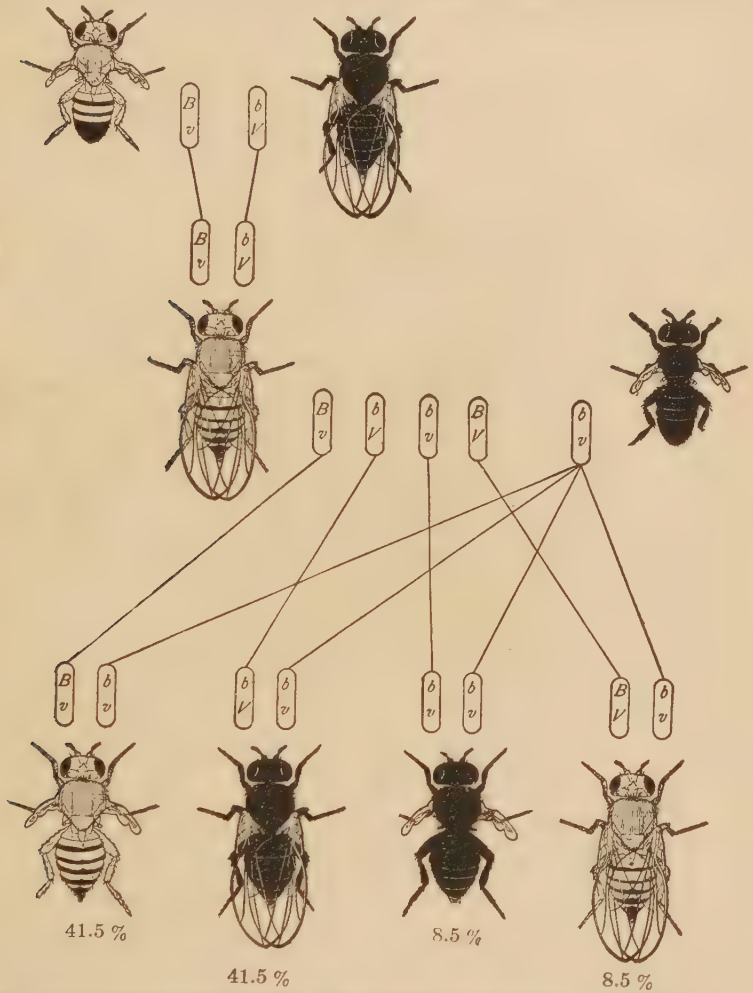

FIG. 218.—Linkage of body color and wing length in the female of Drosophila. Left, above, gray vestigial-winged male; right, black long-winged female. (*From Morgan, Physical Basis of Heredity, J. B. Lippincott and Company.*)

flies, in terms of chromosomes as well as genes, is shown by the two oblong figures above the F_1 fly at the left of the illustration. When such a fly produces germ cells, the number of kinds of germ cells depends on whether it is a male or a female. If it is a male, the two chromosomes always remain intact, and separate at the reduction division, thereby

producing just two kinds of germ cells. These have the formulas *Bv* and *bV* respectively, and are equally numerous. If the fly is a female, the chromosomes behave in this same way in most cells. In some cells, however, the two chromosomes break between the factors for body color and wing shape, and recombine the pieces in the other two possible ways. That is, from chromosomes originally containing *Bv* and *bV* respectively, two new composite chromosomes are made, containing *BV* and *bv* respectively. This breakage and recombination is called *crossing over*, referring to the transfer of the genes from one chromosome to another. A female fly of the F_1 generation therefore produces four kinds of germ cells, while the male produces only two kinds. Figure 218 represents a female in the F_1 generation, and its four kinds of germ cells are shown at the right of the fly.

The four kinds of germ cells produced by such a female fly are not equally numerous. Two of them are much more abundant than the other two. Their numbers may be experimentally ascertained by crossing an F_1 female fly with a black vestigial male (Fig. 218). This male fly, since it exhibits the two recessive characters, must be homozygous for both of them, hence produces but one kind of germ cell (*bv*). The possible unions of four kinds of eggs with one kind of spermatozoön are shown below in Fig. 218, along with the kinds of flies developing from the fertilized eggs. The two at the left, derived from oöcytes in which the two chromosomes remained intact, make up about 83 per cent of the progeny (41.5 per cent of each kind); while the two at the right, derived from oöcytes in which the chromosomes broke and recombined, constitute the remaining 17 per cent of the offspring (8.5 per cent of each kind). From these percentages it is inferred that the four kinds of eggs were produced in the same relative numbers by the F_1 female, and that, therefore, the chromosomes of a female fly remain intact in 83 per cent of all maturing cells, and break between the color and wing factors (cross over) in 17 per cent of the cells.

Determination of Sex.—Closely related to heredity are the phenomena of sex determination. What causes some embryos to develop the organs characteristic of a male, while other embryos that look precisely like them in early stages develop female organs? The answer to this question is not the same for all animals, and for many of them the question is still unanswered. One explanation, however, is applicable to a large number of animals, especially among the insects. This method of sex-determination is as follows.

In most insects the male and female are characterized by different numbers of chromosomes. In certain species of bug the female has 22 chromosomes in every cell of her body, the male only 21. Now, as was pointed out in the chapter on embryology, in the maturation of the germ cells, the number of chromosomes is reduced to half. In the female of

the species here referred to, each mature egg thus receives 11 chromosomes. In the male, with its odd number, an equal division of the chromosomes into two groups is out of the question. Twenty of his chromosomes unite in pairs in the early stages of maturation, and produce ten tetrads. The twenty-first chromosome never pairs with another chromosome, nor produces a tetrad. In one of the maturation divisions it passes undivided to one daughter cell. Figure 219 represents the reduction division. As a result, there are produced two kinds of spermatozoa. Half of them have 10 chromosomes, half of them 11. When an egg (with 11 chromosomes) is fertilized by a spermatozoön having 11 chromosomes, the resulting individual has 22 chromosomes, and becomes a female. When an egg is fertilized by a spermatozoön having 10 chromo-

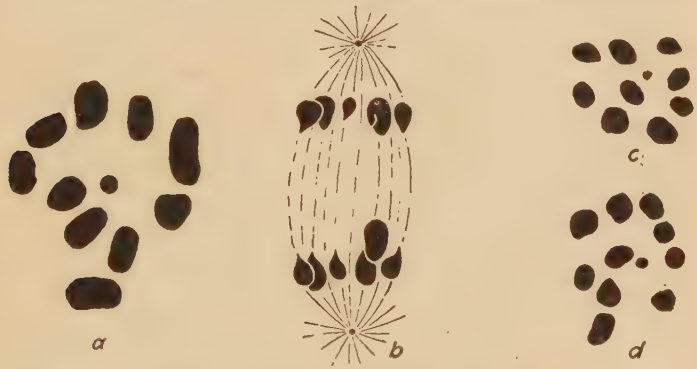

FIG. 219.—The maturation divisions of the male germ cells of the bug Anasa. *a*, polar view of equatorial plate of first division; all the chromatic bodies are double except one, and therefore represent 21 chromosomes, the somatic number; *b*, second maturation division in side view, not all of the chromosomes shown; the single chromosome of *a* is going undivided to the lower pole; *c* and *d*, polar view of the two anaphase groups of the second division; 11 chromosomes go into one spermatid (female-producing), 10 into the other (male-producing). (*After Wilson in Journal of Experimental Zoölogy.*)

somes, the individual developing from the fertilized egg has 21 chromosomes, and is a male. In insects whose sex is determined in this way, at the time of fertilization, all efforts to alter the sex subsequently have failed.

In the above case, the difference in the number of chromosomes is due to the fact that the female has two chromosomes of a particular sort known as the *x-chromosomes*, while the male has only one x-chromosome. In some other animals the number of chromosomes is the same in both sexes, but there is a qualitative difference between them. Thus in the fruit fly Drosophila the female has two x-chromosomes, while corresponding to them the male has an x- and a *y-chromosome*. The latter is morphologically different from the x-chromosome, being bent somewhat like a hook. The x- and y-chromosomes constitute a pair in synapsis, they separate in the reduction division, and two kinds of

spermatozoa are produced, one with an x-, the other with a y-chromosome. Hence sex is determined in essentially the same manner as in species whose sexes differ in the number of chromosomes.

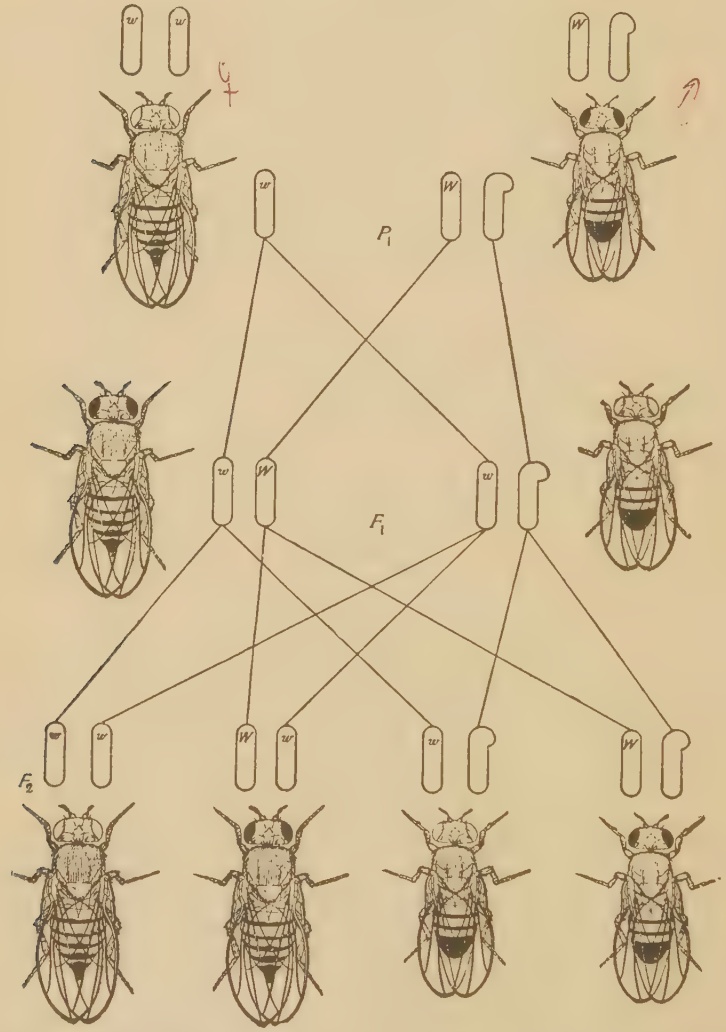

FIG. 220.—Sex-linkage of eye color in Drosophila. Left, above, white-eyed female; right, red-eyed male. (*Modified from Morgan, Sturtevant, Muller and Bridges, Mechanism of Mendelian Heredity. Henry Holt and Co.*)

Sex Linkage.—If the chromosomes associated with sex, as described above, also contain genes for other characters, it is obvious that these characters will be unequally inherited by the two sexes. That this is true is easily demonstrated in the case of white eye in Drosophila. If a white-eyed female is mated with a red-eyed (wild type) male, as shown in

Fig. 220, the offspring consist of red-eyed females and white-eyed males in about equal numbers. (If eye color were not sex-linked all the F_1 flies would be red-eyed.) The F_1 females are red-eyed because red is

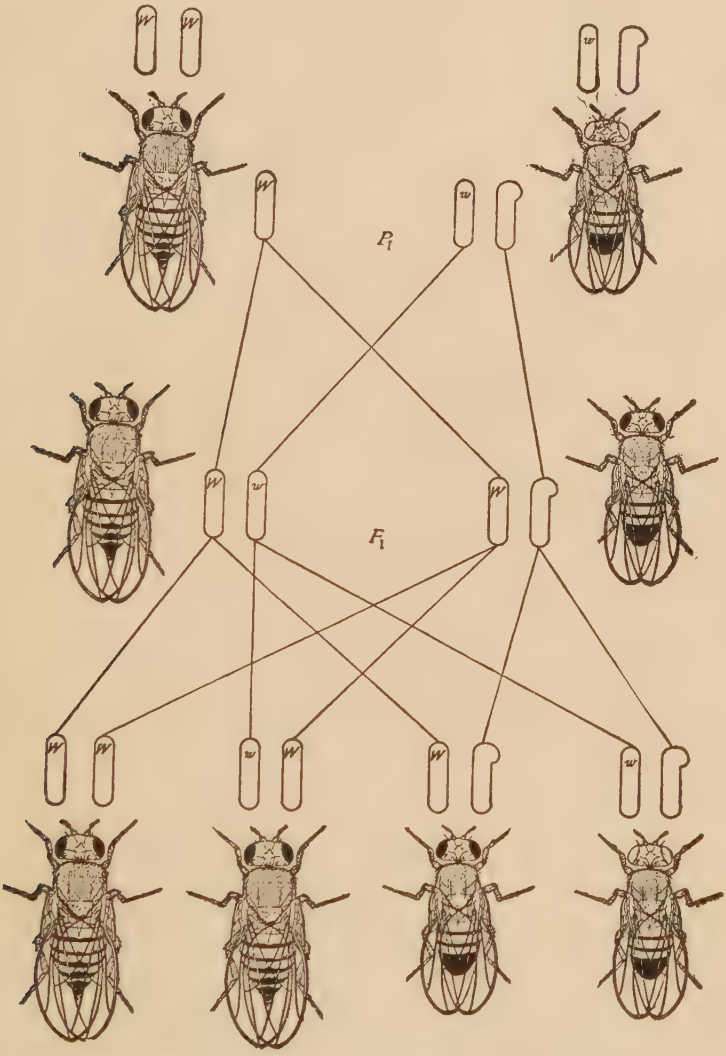

FIG. 221.—Sex linkage of eye color in Drosophila; the reciprocal of the cross in Fig. 220. Left, above, red-eyed female; right, white-eyed male. (*From Morgan, Sturtevant, Muller and Bridges, Mechanism of Mendelian Heredity, Henry Holt and Co.*)

dominant. The males are white-eyed because their y-chromosomes contain no factor which is dominant to white eye, hence the white eye, though recessive, is exhibited. The F_1 flies produce two kinds of germ cells in each sex, as shown in Fig. 220, hence four kinds of F_2 flies are

produced, whose chromosome compositions are shown near the bottom of the figure. Half of the F_2 flies are red-eyed, half white-eyed, whereas if eye color were not sex-linked three-fourths of the F_2 generation would be red-eyed, one-fourth white-eyed.

If the original cross were made reciprocally, that is, if a white-eyed male were mated with a homozygous red-eyed female (Fig. 221), the F_1 flies of both sexes would be red-eyed, and the F_2 generation would consist of red-eyed and white-eyed flies in the ratio of 3:1. Numerically these results are the same as if eye color were not a sex-linked character. However, all the white-eyed members of the F_2 generation would be males, which clearly indicates the sex linkage. A study of Fig. 221 will show, without further explanation, precisely why the results are as stated.

Mechanism of Heredity: a Retrospect.—In the foregoing discussions it has been asserted that the genes are in the chromosomes. The evidence for this statement is abundant, but only a small part of it can be advanced here. In sea urchin eggs, certain chromosomes have been lost in the course of experiments, and with them were lost some of the characters of the larval skeleton. Still better evidence is found in the fact that the chromosomes behave, in maturation, in such a way as to furnish an explanation of many of the fundamental facts of heredity, if only the assumption be made that the genes are in the chromosomes. Some of these fundamental facts may be referred to.

First, the segregation of the genes in the germ cells is accounted for if the genes are in the chromosomes. It has been shown that, in maturation, the chromosomes come together in pairs. Presumably the two genes for a given kind of character are in these two chromosomes. In a heterozygous black guinea pig (*Ww*) the gene *W* is assumed to be in one chromosome, *w* in another. These two chromosomes pair with each other. In a heterozygous rough guinea pig (*Rr*), *R* is in one chromosome, *r* in another, and these chromosomes pair early in maturation. Likewise in a homozygous organism (*WW* or *rr*), the two genes that produce the same character are in different chromosomes, and these chromosomes meet in a pair in maturation. It has also been shown that in one of the maturation divisions the tetrad that is formed by a pair of chromosomes is divided in such a way that the original chromosomes are separated from one another. In this separation is the mechanism by which the genes are segregated —if the genes are in the chromosomes.

Secondly, the phenomena of linkage can be explained if the genes are in the chromosomes. Characters that hang together in their distribution to the germ cells, to a greater degree than would be expected on the theory of chance, are assumed to be represented by genes in the same chromosome. The argument from linkage has been elaborated by a long series of important discoveries since the year 1910 to such a degree that

it now amounts almost to proof that the chromosomes contain the genes. For this evidence, however, the student should consult works on genetics.

What the genes are is largely a matter of conjecture. Since the chromosomes are presumably composed of very complex proteins, it is not unnatural to suppose that the genes are proteins. Some have suggested that they are enzymes. But there is little evidence regarding their nature.

How the genes produce the characters they represent is likewise little understood. It is evident that they influence a long series of chemical reactions (metabolic processes) in the development of the organism. Since the cytoplasm must participate in many of these reactions, objections have occasionally been raised against the view that the genes determine the characters. With the exception of the plastids, however, the cytoplasm appears not to exercise any very specific influence in producing the characters of the adult; it is chiefly a medium in which the genes act, and material out of which the genes produce their characters. Although the cytoplasm exercises no specific influence on the genes, it is probable that interactions among the genes themselves regularly occur. The absence of only one or two of the genes ordinarily present is known, in many cases, to change entirely the characters produced by those that remain. The genes are perhaps, then, not as distinct and independent as the student was led to suppose from the somewhat mathematical accounts of the phenomena of heredity given earlier in the chapter, but are members of a highly organized system.

Definition of Heredity.—Heredity may be defined as the occurrence, in organisms, of any characters due to the nature of the protoplasm of which the organisms are made. Definitions which involve a likeness between parents and offspring have always been objectionable because environmental conditions may intervene to destroy such likeness. Thus, the offspring of a red-flowered Chinese primula will, if reared under ordinary conditions, also produce red flowers. But if these offspring are reared at a high temperature their flowers are white. Heredity has not been destroyed, however, for if the plants are returned to normal temperature they soon begin to produce red flowers again. A definition that involved likeness of parent and offspring would imply the absence of heredity in the case of the primulas. Since, however, the production of white flowers at high temperature and of red flowers at low temperature are both due to the nature of the protoplasm, these flower colors are, by the definition above, inherited.

Variation.—All the knowledge of heredity which we now possess has been made possible through the fact that animals differ from one another in discernible features. Had such differences been wanting, little of the operations of heredity could have been discovered. Characters would have been transmitted in precisely the way they are known to be, but

without individual differences the mode of transmission would have remained unknown. Variation is therefore one of the cornerstones of genetics.

Variation is due to several causes, prominent among them hybridization. It has been shown that, in an F_2 generation, members of the same family differ from one another merely because they contain different genes. When the grandparents differ in only one character, there are only two "varieties" in F_2; when the grandparents differ in two characters, the F_2 generation includes four visibly different combinations, as was seen in the case of rough, smooth, black, white in guinea pigs. When many differences between the grandparents are involved, the F_2 presents exceedingly numerous possibilities.

The differences involved in such cases must, however, have had an origin. If it is true that animals have reached their present condition by a process of evolution, a thesis that is developed in the last several chapters of this book, it is inconceivable that this change has been brought about merely by the recombination of genes in different ways. It is inconceivable that the earliest organisms, whatever they were like, contained genes for all the characters that are now possessed by their descendants, only waiting to be shaken and thrown like dice to produce the combinations now known. Changes must have been introduced in some other way. There is, moreover, abundant evidence of changes of this kind that have been recognized in specific cases. A number of years ago a white-eyed fruit fly appeared in cultures comprising thousands of individuals, every other fly in which was red-eyed. Furthermore, every ancestor of this white-eyed fly for scores of generations had had red eyes. New characters appearing suddenly in this manner are called *mutations*. The common evening primrose Œnothera is every year producing plants unlike their parents. Many of these new characters arising in the evening primrose may be due to recombinations of genes already present; but it is hardly to be doubted that the differences arose in the first place as mutations. Scores of other examples of supposed mutations could be cited, though the evidence that they are mutations is not in every case so clear. Variations of this kind are strictly inherited. Indeed, the requirement of inheritance is part of the definition of the word mutation.

The nature of mutations can only be surmised. They must be due to modification of the genes. If the genes are complex chemical substances, as suggested above, changes in their structure are very probable, but nothing is actually known about such changes.

Certain kinds of variation are due to another cause, namely, the environment. It is seldom that two organisms occupy exactly the same kind of environment. Points in the same pond are unequal in available food, in amounts of dissolved gases, in temperature, in light, in predatory animals. The eggs from which animals hatch are unequally provided

with yolk, and this is essentially a condition of the young animal's environment. Differences in parental care after birth or hatching may produce differences in the adult. Such effects of the environment, however, are probably not in any case among higher organisms, or at most only rarely, inherited. With them the geneticist has little to do, except to guard against being deceived by them.

Practical Applications of Genetics.—Although genetics as a science is comparatively young, it has already yielded results in the development of domesticated animals and plants that are of economic value. These results have been more simple and clear in the case of plants than in that of animals, though the end products have been scarcely more valuable. Inheritance in animals is very complex in nearly all characteristics which are of commercial worth, and the practice of the breeder is still very largely the method of trial and error. But even by this empirical method the milk-production of cattle, the egg-laying qualities of poultry, the wool-clip of sheep, the productivity of the silkworm and many other economic features of animals have been marvelously improved. In plants the economically important features are more often inherited in simple fashion, and it is possible to apply promptly the principles of heredity which have been elaborated since 1900. By these means the productivity of wheat and other grains has been appreciably increased. It has been possible to combine in one variety of wheat, for example, such desirable qualities as high yield, stiff straw, winter hardiness, and resistance to rust; in oats, high yield with the absence of hulls; in tobacco, high number and desirable shape of leaves with proper texture and "grain." The prospects for further valuable improvements are bright.

In human beings the application of the knowledge of heredity has scarcely begun. Progress has been slow for the reason that such application must either be voluntary, which requires much education of the public, or must be enforced by legislation, which always meets with objections from those to whom "personal liberty" is dear. Furthermore, less is definitely known of heredity in man than in domestic animals, because knowledge can only come from family histories, not experiments, and family records can seldom be traced for many generations. While much that is known could well be applied voluntarily by intelligent people, successful legislation must be limited for the present to those characters which are of the greatest social importance and whose heredity is best known, such as feeblemindedness.

Problems for Drill in Genetics

1. A rose-combed fowl (Fig. 216, *B*) mated with a single-combed fowl (Fig. 216, *C*) produces only rose-combed offspring. State the expectation in F_2, and give the formulas of all individuals and all germ cells for each of the three generations, beginning with the original parents.

9:3:3:1

2. Tall peas are dominant over dwarf peas. What would be the formula of F_1 plants? Their appearance? If the F_2 generation included 17 dwarf plants, how many tall plants should there be in that generation?

3. Mating a red-eyed and a pink-eyed fly yields red-eyed offspring. If one of these red-eyed offspring is mated to its pink-eyed parent, what will be the nature of their progeny?

4. Brown color in mice is dominant over albinism. In a given cross between a brown mouse and an albino, six of the offspring were brown, five albino. What was the nature of the original brown parent?

5. A long-winged fruit fly mated with one having vestigial wings produced 28 long-winged and 23 vestigial offspring? What were the formulas of the parents? Of their long-winged offspring? Of their vestigial-winged offspring?

6. Snap-dragons with bilaterally symmetrical flowers, crossed with plants with radial flowers, produce only bilateral F_1. If an F_1 plant is self-fertilized, what is the chance that one of its offspring selected at random will be radial?

7. Shepherd's purse with triangular seed capsule is dominant over the variety with spindle-shaped seed capsule. What is the appearance of a heterozygote with respect to shape of seed capsule? What would be the result of mating a heterozygote with a homozygous plant having triangular capsules?

8. Starchy grain is dominant over sugary grain in corn. If, in a cross between these types, 58 of the progeny are sugary, how many of the progeny should be starchy?

9. A certain white-fruited squash, self-fertilized, produced some white and some yellow offspring. If there were 21 yellows, how many whites would be expected?

10. Short hair is dominant over long hair in guinea pigs. A short-haired guinea pig, one of whose parents was long-haired, was mated with a long-haired animal. What is the expected nature of their offspring?

11. The offspring of a brown mouse and an albino are all brown. What types of mating would produce only brown offspring? Only albino offspring?

12. The progeny of purple corn and white corn are purple. What would be the result of crossing one of the purple offspring with the purple parent type? How many of the progeny would breed true if self-fertilized?

13. A fly that is heterozygous for gray and black color is gray. What would be the nature of the progeny of a homozygous gray mated with a homozygous black fly? What would be the result of mating together two of their offspring? Which offspring of the last cross could be expected to breed true if mated to others visibly like them?

14. A cross between polled (hornless) and horned cattle yields polled offspring. What would be the progeny of two of the polled offspring?

15. How could you determine whether a polled cow is heterozygous or homozygous?

16. Trotting in horses is dominant over pacing. Describe the inheritance of these characters through the F_2 generation, and explain by means of formulas of all individuals and all germ cells.

17. Of the following animals, taking into account only the contrasts with other characters afforded by the foregoing problems or the chapter on Genetics, which ones could be declared homozygous without testing: albino guinea pig, brown mouse, pink-eyed fruit fly, radial snap-dragon, triangular shepherd's purse, long-haired guinea pig, starchy corn?

18. Mating a red-eyed fly with curved wings and a brown-eyed fly with straight wings yields an F_1 all red-eyed and straight-winged. What kinds of flies would you expect in F_2? In what relative numbers?

19. Pea comb in fowls is dominant over single, and frizzled feathers (turned up at end) are dominant over smooth (straight) feathers. If a single-combed smooth fowl is mated with a pea-combed frizzled fowl, what is expected in F_1 and F_2? Give explanation including formulas of all individuals and germ cells.

20. A rough-coated black guinea pig, whose mother was smooth and white, is mated with a smooth white animal. What kinds of offspring should they produce, and in what relative numbers?

21. Self-colored rats (color distributed over the body) are dominant over hooded (color only on head, rest of body white). Albino rat is recessive to gray. Crossing a homozygous gray hooded rat with an albino having a pair of genes for self-color (which of course cannot show in an albino) would produce what result in F_1? What in F_2? Of 80 F_2 animals, how many should be of each visibly distinguishable kind?

22. Assigning the formula *PPrr* to a pea-combed fowl, and *ppRR* to a rose-combed fowl, show which individuals of the F_2 generation from a cross between these two kinds have walnut, pea, rose, and single combs.

23. The genes for purple eye (normally red) and curved wings (normally flat) in Drosophila are in the same chromosomes, and the normal red eye and flat wings are dominant. A homozygous purple-eyed flat-winged fly is crossed with a homozygous red-eyed curved-winged fly. One of their daughters is mated with a purple, curved male. What kinds of offspring will they produce, and in what proportions, assuming that 21 per cent of the pairs of chromosomes break between the factors for eye color and wing shape?

24. Each cell of the muscles of a male bug contains 27 chromosomes. How many chromosomes in its spermatogonia? How many in its mature spermatozoa? How many chromosomes in the body cells of the female of the same species? How many in her mature eggs? How many in fertilized eggs?

25. Formulate the cross between a white-eyed male Drosophila and a homozygous red-eyed female, described in the text, to show why the white-eyed F_2 flies are all males.

26. Color-blindness is a sex-linked recessive, and sex in man is determined essentially as in Drosophila. A girl of normal vision whose father was color-blind marries a color-blind man. What will be the nature of their children?

27. In four-o'clocks the red-flower color is not wholly dominant over white, so that heterozygous flowers (*Rr*) are pink. What would be the appearance of the offspring of a self-fertilized pink-flowered plant? If the progeny of this plant numbered 100, how many should there be of each kind?

28. In shorthorn cattle, the hybrid between red and white is roan (having white hairs and red hairs intermingled). What would be the nature of the offspring of a roan and a white animal? The offspring of a roan and a red animal?

29. A horned roan shorthorn cow is mated with a homozygous polled white bull. What chance has their offspring of being (1) polled red, (2) polled white, (3) horned white? (See Problems 14 and 28 for the inheritance of these characters.)

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CHAPTER XIII

CLASSIFICATION OF ANIMALS

Taxonomy (from the Greek *taxis* = arrangement and *nomos* = law) is literally an orderly arrangement. As applied to living things it refers to the classification of animals and plants on the basis of fundamental similarities. The taxonomy of animals, with which this chapter deals, is wholly distinct, except in principle, from that of plants, though the simplest members of the plant and animal kingdoms are not readily distinguishable from one another. Zoölogical taxonomy is often called *systematic zoölogy*.

Conceptions of Taxonomy.—An orderly arrangement of objects or facts presupposes a system of classification, and the same objects or facts can usually be classified in different ways by the use of different characters, qualities or relations as a basis. Moreover, different systems of classification may be adopted to suit particular purposes or to satisfy particular bents of mind. Thus because it is possible to classify animals in different ways, taxonomy has often been considered a mere cataloging of animal forms, and it has been assumed that the purpose of taxonomy is merely to find a way in which the forms may be *conveniently* arranged, described, and cataloged. This conception is erroneous, but to state wherein lies the error requires that the aims of those who propose the various systems be compared. Much of this comparison must await the historical account below. It may be pointed out here, however, that all but one of the systems of classification that have ever been in use have been essentially devices to save confusion. Things were put upon shelves, figuratively, and labeled and cataloged and perhaps cross-cataloged. So long as prevention of confusion was the chief aim, it made little difference whether the shelves were numbered in vertical columns or in horizontal rows. Every classification which sought nothing more than convenience might therefore be artificial and arbitrary, and one person's classification might be quite as good as another's. The one exception to this arbitrary basis of arrangement is found in the system of classification that prevails at the present time. The modern system serves two purposes, instead of but one. It has grown up largely since the general acceptance of the evolution doctrine, according to which species of animals are related to one another through common descent,

Classification may now insure the convenience that was desired in the earliest attempts at organization, and at the same time express the kinship which the evolution doctrine implies. The advantages of a system which serves this double function are so great that it is now recognized that there can be but one true and natural basis for taxonomy, and this lies in the genetic relations and the successive steps of divergence from the more or less generalized types. Far, then, from being a mere cataloging or describing of animals, systematic zoölogy is concerned with the estimating of the relative importance of all structural details, the habits,

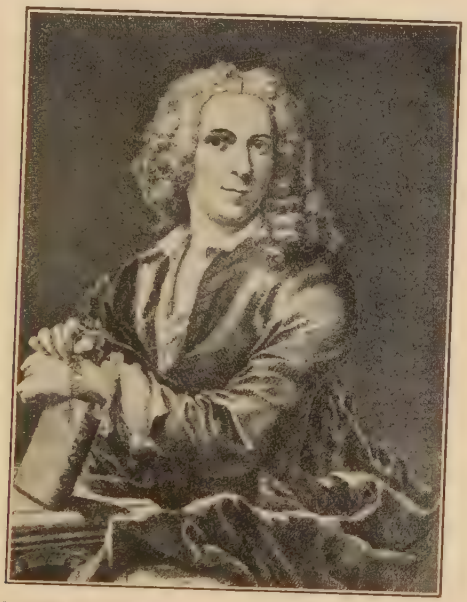

FIG. 222.—Carl von Linné (Carolus Linnæus), 1707–1778, at the age of forty. (*Courtesy of New York Botanical Garden.*)

and the distribution of the forms, as evidence from which the pedigrees may be reconstructed and expressed.

Ray and Linnæus in Taxonomy.—It has been said that John Ray (1627–1705), an Englishman, was the first true systematist. Ray proposed a dichotomous systematic table of the animal kingdom, that is, a system which branched by twos, and distinguished by anatomical characters several groups now recognized as natural ones. It is Carolus Linnæus (Carl von Linné, Fig. 222, 1707–1778), however, who is considered to be the real founder of classification. Linnæus's most important work was the "Systema Naturæ," which appeared in twelve editions between 1735 and 1768 and, after his death, in a thirteenth, edited by Gmelin. In this work Linnæus completed a classification which Ray had

established in part, giving names to important groups that Ray had left without appellations, and describing animals in language which, unlike many of the writings of his time, could not be misunderstood. Linnæus also had the courage to defy prejudice in such details as removing the whales from the group of fishes, to which Ray also knew they did not belong, and placing them with the terrestrial hairy animals called mammals. For in the Linnæan classification structural characters, rather than habits or external forms, were used as a basis. Six *classes* were employed, four of them vertebrate (borrowed from Ray) and two invertebrate. These classes were divided into *orders*, the orders into *genera* and the genera into *species*. The lesser groups were usually much more inclusive than the groups now given the same nominal rank. Thus, a Linnæan genus occasionally includes three or four orders, as these groups are now reckoned. Moreover, the genus often contained animals now placed in widely separated categories. One genus was erected to include certain sea cucumbers, a worm, a colonial jellyfish, and several primitive near vertebrates; some of these are now placed near the bottom, others near the top, of the animal scale. However, since Linnæus did not hold any evolutionary views, such discrepancies did not trouble him.

Later Temporary Systems of Classification.—Following Linnæus, many naturalists concerned themselves with systematic zoölogy. Some of them adopted the Linnæan system in general, but altered it to suit their tastes, sometimes improving it but quite as often not. Others invented new classifications. Georges Cuvier (1769–1832) established four major groups, called branches, which he divided into classes, nineteen in number; and some parts of his classification remained in vogue in his own country for three-quarters of a century. Superior to Cuvier in his conceptions was de Blainville (1777–1850) who in several instances happily discovered the structural characters that were of genuine importance in distinguishing natural groups. He proposed a classification involving three subkingdoms, distinguished by the arrangement of their parts about a center or axis. These subkingdoms were the *Artiomorphes*, having a bilateral form like the majority of animals; the *Actinomorphes*, with a radiate form like a starfish; and *Heteromorphes*, animals having an irregular form (chiefly protozoa and sponges). Lamarck (1744–1829) devised a classification based upon nervous sensibility, and proposed three principal groups: the *apathetic* animals, those without nervous systems or apparent sensation among the invertebrates; the *sensitive* animals, also among the invertebrates; and the *intelligent* animals corresponding to the vertebrates. Oken (1779–1851), who was a philosopher rather than a naturalist, advocated simultaneously at least two classifications, which were equally worthless. One divided animals into groups according to their systems of organs, as intestinal, muscular,

sexual, respiratory, vascular, etc. His other classification was based on the senses. Thus, there were the *Dermatozoa* (literally, skin or touch animals), by which he meant the invertebrates; the *Glossozoa* (literally, tongue animals), the fishes; the *Rhinozoa* (nose animals) which included the reptiles; the *Otozoa* (ear animals), or the birds; and another class, which appears to have been called interchangeably the *Ophthalmozoa* (eye animals) or *Thricozoa* (hair animals), the mammals. It would be hard to name a set of distinctions less applicable as classification marks than most of these, but Oken did not engage in practical matters. Mention may also be made of the systematic work of Pierre Latreille (1762–1833), Johannes Müller (1801–1858), and Louis Agassiz (1807–1873). Then there was a host of minor systematists the value of whose labors has been diminished by attempts to force their classifications into some numerical system, as for example those who held that the number of orders in each class should be the same as the number of families in each order, or the number of genera in each family. The favored number was five in some classifications, less often three, four or seven.[1]

These early modes of arrangement of animals have been described, not for any value that may attach to them as classifications, but to form a background for the one system that has survived. It should be obvious, from the brief statements made, that most of the plans used were totally unsuited to the requirements which later developments of zoölogy would have imposed upon them. The system of Linnæus, however, was happily capable of being adapted to the demands of the tenets of evolution, and it alone has persisted to the present time.

The Linnæan System.—That the Linnæan system was rapidly adopted and is now universally employed by zoölogists is doubtless due largely to the fact that it introduced a sharply defined grouping, a definite terminology, and brief, clear diagnoses; that it permitted early naturalists to group those forms that resembled each other; and that it equally well permitted the classification of forms according to their relationships. As stated above Linnæus recognized groups of four different values—the class, the order, the genus (plural, genera), and the species (plural, species). To these categories have been added the *phylum* (plural, *phyla*) and *subphylum* (assemblies greater than the class), the *subclass*, the *suborder*, the *family*, the *subfamily*, the *subgenus*, the *subspecies* and others. Of these additional groups the phylum and family are now generally accepted, and the others are used for some groups or by some naturalists. The rank of recognized categories may be expressed as follows:

[1] For many of the facts regarding these old attempts at classification we are indebted to Theodore N. Gill, Annual Report of the Smithsonian Institution for 1907.

Phylum. Example, *Chordata* (the chordates)
Subphylum. Example, *Vertebrata* (the vertebrates)
Class. Example, *Mammalia* (the mammals)
Subclass. Example, *Eutheria* (the placental mammals)
Order. Example, *Rodentia* (the rodents)
Suborder. Example, *Sciuromorpha* (the squirrel-like rodents)
Family. Example, *Sciuridæ* (the flying squirrels, marmots, squirrels and chipmunks)
Subfamily. Example, *Sciurinæ* (the marmots, squirrels and chipmunks)
Genus. Example, *Sciurus* (the arboreal squirrels)
Subgenus. Example, *Tamiasciurus* (the red squirrels)
Species. Example, *hudsonicus* (the Hudsonian red squirrel)
Subspecies. Example, *loquax* (the southern Hudsonian red squirrel)

In some groups "divisions" or "sections" are recognized by authors, but these categories have no definite place in the system; that is, they may be introduced to mark off a group of genera, an assemblage of orders, etc.

The Linnæan system designates the species by two Latin or latinized names, the *generic* name, a noun, and the *specific* name, usually an adjective. Thus Natrix is the generic name of a group of water snakes, and *Natrix rhombifera* and *Natrix sipedon* are two species of water snakes. This is known as the binomial system of nomenclature. When subspecies are recognized three names are used, the generic, the specific and the subspecific, thus, *Thamnophis sirtalis parietalis*. The term "variety" is usually considered synonymous with subspecies in taxonomy, but it may be used to indicate divisions smaller than subspecies, and in one group, the ants (family Formicidæ), the systematists regularly recognize and designate divisions smaller than subspecies by name, using four names for each variety (for example, *Camponotus herculeanus ligniperdus noveboracensis*, the northern carpenter ant).

Rules of Nomenclature.—The binomial and trinomial systems of nomenclature have been of great convenience to naturalists. Before their adoption common names were in use in the scientific world and led to much confusion, the same animals being known by different names and different animals by the same name. To make certain that each animal shall have but one scientific name and that no two animals shall have the same name, rules of nomenclature have been proposed at different times for the purpose of determining which name shall prevail when several have been or are likely to be inadvertently proposed for the same form. Linnæus seems to have appreciated the necessity for rules and to have proposed a set. These rules were not sufficient, and several other codes were proposed, the more important of which were the *British Association Code*, the *American Ornithological Union Code*, the *Code of the German Zoölogical Society*, and the *Code of the International Zoölogical Congress*

The code now almost universally in use is the *International Code of Zoölogical Nomenclature*, adopted by the International Zoölogical Congress and governed through a Commission on Nomenclature.

The International Code.—Some of the essential features of the International Code are as follows. The first name proposed for a genus or species prevails on the condition that it was published and accompanied by an adequate description, definition, or indication, and that the author has applied the principles of binomial nomenclature. This is the so-called *law of priority*. The tenth edition of the "Systema Naturæ" of Linnæus is the basis of the nomenclature. The author of a genus or species is the person who first publishes the name in connection with a definition, indication or description, and his name in full or abbreviated is given with the name; thus, *Bascanion anthonyi* Stejneger. In citations the generic name of an animal is written with a capital letter, the specific and subspecific name without initial capital letter. The name of the author follows the specific name (or subspecific name if there is one) without intervening punctuation. If a species is transferred to a genus other than the one under which it was first described, or if the name of a genus is changed, the author's name is included in parentheses. For example, *Bascanion anthonyi* Stejneger should now be written *Coluber anthonyi* (Stejneger), the generic name of this snake having been changed. One species constitutes the *type* of the genus; that is, it is formally designated as typical of the genus. One genus constitutes the type of the subfamily (when a subfamily exists), and one genus forms the type of the family. The type is indicated by the describer or if not indicated by him is fixed by another author. The name of a subfamily is formed by adding the ending *-inæ*, and the name of a family by adding *-idæ* to the root of the name of the type genus. For example, Colubrinæ and Colubridæ are the subfamily and family of snakes of which Coluber is the type genus.

The Basis of Classification.—Early systematists largely employed superficial characters to differentiate and classify animals, and their classifications were thus largely artificial and served principally as convenient methods of arrangement, description, and cataloging. Since the time of the development of the theory of descent with modifications by Lamarck (1809) and Darwin (1859), there has been an attempt to base the classification on relationships. Very nearly related animals are put into the same species. They are related because they descend from a common ancestry, and that common ancestry could not in most cases have been very ancient, otherwise evolution within the group would have occurred and the species would have been split into two or more species. Species that are much alike are included in one genus, being thus marked off from the species of another genus. The similarity of the species of a genus is held to indicate kinship, but since there is greater diversity among the individuals of a genus than among the members of a species,

the common stock from which the species of a genus have sprung must have existed at an earlier time, in order that evolution could bring about the degree of divergence now observed. In like manner, a family is made up of genera which resemble one another more than they resemble other genera, and their likeness is again a sign of affinity. But to account for the greater difference between the extreme individuals belonging to a family, evolution must have had more time; that is, the common source of the members of a family must have antedated the common source of the individuals of a genus. Orders, classes, and phyla are similarly regarded as having sprung from successively more remote ancestors, the time differences being necessary to allow for the differences in the amount of evolution. This statement is in general correct. However, since evolution has probably not proceeded at the same rate at all periods, nor in all branches of the animal kingdom at any one time, the time relations of the groups of high or low rank must not be too rigidly assigned. Thus certain genera, in which evolution has been slow, are probably much older than some families in which evolution has been rapid. It is not improbable, also, that some genera are quite as old as the families which include them; but in no case can they be older. Furthermore, different groups are classified by taxonomists of different temperaments, so that groups of a given nominal rank may be much more inclusive (and hence older) in one branch of the animal kingdom than in another. On the whole, nevertheless, the groups of higher rank have sprung from ancestry more remote than that of the groups of lower rank.

The means of recognizing the kinship implied in classification permit some differences of opinion. It is recognized that likeness in structural characters is the chief clue to affinities. However, the evidential value of similarity in one or several structures unaccompanied by the similarity of all parts is to be distrusted, since animals widely separated and dissimilar in most characters may have certain other features in common. Thus, the coots, phalaropes and grebes among birds have lobate feet but, as indicated by other features, they are not closely related; that is, the lobes on their feet are *analogous*, meaning that they serve the same function. Analogy is widespread in the animal kingdom, since the same activities must be carried on by animals of very different structure. Locomotion, for example, is effected by legs of very different kinds. The legs of a kangaroo, a crayfish, and a honeybee (Fig. 223) are analogous, but their structure is unlike. The skeleton is within the flesh in the first of these, but on the outside in the other two and the materials of the skeleton are different. The crayfish and the bee, though alike in the position of the skeleton, differ in the number and character of the segments of the leg. Another case of analogous structures is that of lungs and gills (Fig. 224). Both are used for absorbing oxygen, but are wholly different in structure.

The foregoing analogous organs are so unlike in structure that no one would be led to classify together the animals that possess them. Not always, however, are the structural differences so great. A whale swims by means of paddles and a flattened tail which greatly resemble fins, and the early naturalists regarded whales as fishes. Yet the whale is a warm-blooded air-breathing animal with a four-chambered heart and

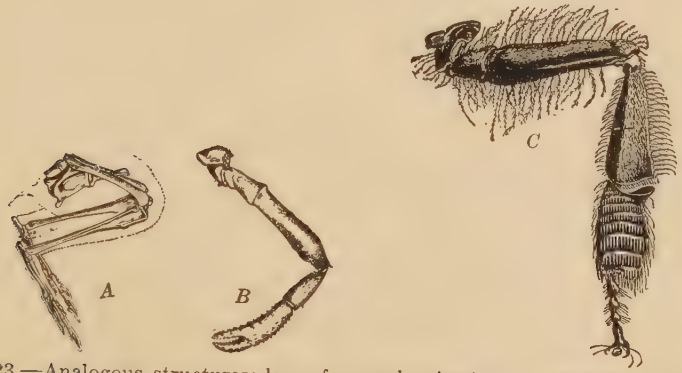

FIG. 223.—Analogous structures; legs of several animals. *A*, kangaroo; *B*, crayfish; *C*, honey bee. (*C from Metcalf and Flint, Destructive and Useful Insects, McGraw-Hill Book Company, Inc.*)

some hair on the skin, and has also the other characters of mammals. A close resemblance is also exhibited by certain lizards (Amphisbænidæ) to a group of snakes (Typhlopidæ), because the former are blind and legless and have a short tail. These external similarities have apparently arisen in evolution independently of one another, and for that reason are not an indication of kinship.

FIG. 224.—Analogous structures; respiratory organs. *A*, gills of salamander; *B*, lung of frog. (*From Wieman, General Zoology, McGraw-Hill Book Company, Inc.*)

Homology.—In judging of kinship by means of structural similarities, therefore, care must be taken to employ only those structures that have had similar origins in evolution. It is sometimes difficult to determine now whether similar structures in two groups of animals arose in evolution in the same way, or whether they have converged, for some reason, from originally distinct beginnings. In general, if two or more

groups of animals have only one or a few structures in common while all or most others are different, it is safer to assume that the common structures arose independently, or at least that their recent evolutionary developments have been independent, and that the groups are therefore not closely related. The lobate feet of the several groups of birds mentioned above fall in this category. If, however, a great many features of two groups of animals are closely similar, the probability is that such similarities could only have come from similar or identical origins in evolution. The work of the taxonomist therefore becomes, in large measure, the recognition of those characters in different animals whose similarities are due to common evolutionary origin.

Structures that arise in the same way in evolution are said to be *homologous* with one another, or to exhibit *homology*. The term homology may be defined as similarity of origin in evolution. Unfortunately for the taxonomist the early evolution of the structures on which his classifications is based took place in many instances probably millions of years ago. How can he ascertain, under these circumstances, whether the evolution of structures in two animals was similar or not? The answer to this question must usually be arrived at indirectly.

Homology Judged from Adult Structure.—The most reliable means of judging of similarity of evolution in two groups would be fossil members of those groups, if fossils could be obtained in sufficient numbers to establish a fairly complete history extending far back into their ancestry. Some such histories are given in Chap. XVI. In most families of animals, however, such fossil series are wanting, and the taxonomist must rely on what can be discovered from the living animals of today. In clear cases adult structure is sufficient, but only where many features are alike in the animals in question. A classical case of homology, judgment of which could safely rest on adult structure alone, is that which exists among the fore limbs of vertebrate animals (arms, wings, fore feet, etc.). Although the external forms of these fore limbs differ greatly in birds, seals, horses, whales, bats, and man, their skeletons are found to correspond very closely, bone for bone, at most points. It is believed that so many similarities could not be the result of accident, or of convergence from originally distinct sources, and that the likenesses are a sign of similar evolutionary origins. The nervous systems of vertebrate animals are equally good examples. The parts of the brain in fishes, amphibia, reptiles, birds and mammals have a very obvious correspondence, and the origin and distribution of the cranial nerves is very similar in all of them. It is scarcely conceivable that these nervous systems could be alike in so many respects unless their evolutionary histories were largely the same.

Homology Ascertained from Embryonic Development.—Somewhat better evidence of homology than is afforded by adult structure can often

be obtained from a knowledge of embryonic development. As was pointed out in Chap. XI, corresponding structures in vertebrate animals arise in essentially the same way in the embryo. The nervous system of one vertebrate begins with ridges that are much like those of any other vertebrate embryo. The eye of a bird develops as does the eye of a frog. The early ear also is about the same, whether found in a reptile or a mammal. This similarity of the first appearance of embryonic structures occurs even when the adult organs are strikingly different. The arm of a man and the wing of a bird are different from one another in the adult condition, especially in the hands; but in the embryo the earliest limb buds are almost identical. An even greater difference exists between the adult fore and hind limbs of a bird. When compared, bone for bone, there is scarcely a point at which there is not a distinct difference. Yet the wing and leg could be interchanged in the early embryo, and few persons would detect the substitution. Thus, on the whole, animals whose adult structure is similar resemble each other even more closely in embryonic stages. In some instances the adult structures of two animals have become so changed as to lose all similarity, yet the resemblance in the embryos persists. An example of this kind is found in the parasite Sacculina described in Chap. XVII. Biologists believe that similarity of structures in the embryo can only be due to similarity of the evolution of those structures; and because resemblance in the embryo remains after adult similarity has been diminished or destroyed, embryonic development is regarded as better evidence of homology than is adult structure.

Origin of Homology.—Homology is presumably no accident. The discussion in the chapter on evolution may be anticipated by stating the conclusion of biologists that homology results from the inheritance of a common ancestral condition. All animals now possessing organs homologous with one another must have descended from a common ancestral form. The organs of the present day descendants of that ancestor arise in the same way in the embryo, because in some fundamental respect the organs of the ancestor arose in that manner. The adult structure is similar in all these descendants because that structure has been inherited, with modifications, it is true, from the common ancestor.

Biogenetic Law.—The evident dependence of homology upon a common descent led, a few decades back, to a conception comprised under the term *Biogenetic Law* sometimes called by the more expressive and less committal name *Recapitulation Theory*. According to this law, or theory, the embryonic stages of animals of today represent the condition of successive ancestors of these animals. That is, early embryonic conditions represent very remote ancestors, later embryonic stages represent more recent ancestors. Some biologists held that the early

embryonic stages are like the adult ancestors, others believed merely that the embryonic stages of the present are like the embryonic stages of the ancestors.

If this law were capable of rigid application, it would be easy to trace the evolutionary history of a race simply by studying its individual development. In some cases, this simple procedure is almost feasible. A series of fossil cephalopods (allies of the cuttlefishes), described in Chap. XVI, is a case in point. The fossil remains of these animals indicate that, in their racial history, their shells were at first provided with straight partitions, later with partitions whose edges were bent, crooked and finally lobed in a very complicated manner. Since in the fossils both the young and old stages of each individual shell are preserved it is possible to compare the individual development with the racial development. When this is done, it appears that the individuals of the highly complex types passed through very similar stages, in which the partitions were first straight, then bent, crooked, and finally complicated.

In most animals, however, embryonic development has undergone a good many changes, so that steps in development no longer represent accurately the steps in the evolution of their ancestors. That is, the biogenetic law is less generally applicable than it was formerly supposed to be. However, many important facts of evolution, of limited scope, have been discovered by an appeal to this law. A case in which the recapitulation theory is plainly correct is in the development of gill pouches in all of the vertebrates. Gills are never developed in the reptiles, birds, and mammals; but gill pouches are formed, and these may actually open temporarily to the outside as gill clefts, between which are the gill bars upon which gills are developed in fishes and amphibia (frogs, toads, etc.). The production of gill pouches and bars in the higher vertebrates as well as in the lower, besides indicating a common ancestry of all these animals, points with much certainty to the conclusion that the ancestor was a fish-like animal—fish-like at least to the extent of being aquatic and respiring by means of gills.

Requirements of a Genetic Classification.—It will be obvious from the foregoing discussion what use of homology may be made in the taxonomic arrangement of animals. Putting into one group animals whose structures are homologous with one another insures not only that members of the group resemble each other, but that they are related. It insures that they are actually cousins in the ordinary sense. Practically all the old classifications brought together animals that are similar to some extent; but, as was pointed out above, not all similarity has resulted from common descent. If the taxonomist can discover the similarities that are inheritances from a common ancestor, and ignore those resemblances that arise from other causes, his system of classification can rest

upon kinship alone. That is what is attempted in modern taxonomy, and the value of the classification depends upon the success with which the distinction between homologous and non-homologous characters is made. A classification based solely upon descent, and hence kinship, may be called a genetic classification. The modern system is sometimes also called a natural system because it has a fundamental basis in nature, as distinguished from arbitrary or artificial systems. Since a genetic classification must take into consideration the entire animal, the search for affinities becomes an attempt to evaluate the results of all morphological knowledge, and it is also becoming evident that other things besides structure may throw light upon relationships. The fossil records, geographical distribution, ecology, and experimental breeding may all assist in establishing affinities.

The Method of Taxonomy.—It is evident that before the relationships of animals can be determined the forms must be known, for unknown forms constitute breaks in the pedigrees of the groups to which they belong. Moreover, as pointed out above, the structural characters, variation, and distribution must be known before a form can be placed in the proper place in a genetic system. For these reasons an important part of systematic work is the description of forms and an analysis of their differences. After the Linnæan system was adopted zoölogists attacked this virgin field and for many years "species making" predominated. Even at the present time when other aspects of zoölogy have come to receive relatively more attention it is an interesting fact that the analytical method prevails in systematic studies, and taxonomy suffers from, and in part merits, the criticism that it is a mere cataloging of forms and ignores the higher goal of investigation, namely the discovery of the course of evolution. Many systematists, however, recognize that the ultimate purpose of taxonomic work is to discover the relationships as well as the differences between the described forms in order that the course of evolution may be determined. In other words, it is appreciated that while analytical studies are necessary they are only preliminary, and that upon their results must be built synthetic studies, if taxonomy is to fulfill its purpose.

The Difficulties of Taxonomy.—One of the greatest obstacles to a genetic classification of animals is the incomplete fossil record of extinct forms. The comparative poverty of records makes it necessary to determine the breaks in the chain as well as possible until such a time as they shall be closed by additions to the data of paleontology. A further difficulty lies in the nature of the material. The structure of animals is so complex and variable, and the distribution and ecology are so complicated, that the task of making analyses which will permit a satisfactory grouping is a laborious one. The enormous number of forms

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is another difficulty. So many forms have been discovered and so many apparently await discovery, study, and description, that systematic zoölogists must generally limit their work to some one or two orders and in some cases to a single family. To distinguish the workers on the different groups of animals different names have been applied. Thus, one who is engaged with the protozoa is a *protozoölogist;* the student of worms is a *helminthologist;* of the mollusks, a *conchologist;* an *entomologist* deals with insects, a *herpetologist* with reptiles or Amphibia or both, an *ornithologist* with birds, and a *mammalogist* with mammals. These names do not, however, imply an interest in classification alone, since an entomologist may be concerned with ecology and a conchologist with geographical distribution, etc.

Relations of Taxonomy.—Classification has wide connections with nearly all other phases of biology. In a practical manner every biologist has occasional or frequent use for the technical knowledge of the systematist, and this requirement is not a purely formal one. Many investigations whose principal aim is entirely apart from classification must nevertheless constantly use the data of taxonomy. Thus the zoögeographer, as will be apparent in Chap. XV, is not primarily interested in classification; but in order to discover the principles which have guided migration or determined extinction in the past he must be thoroughly conversant with the taxonomy of the group whose distribution he studies. The paleontologist also requires a knowledge of classification, not only of extinct forms but of their living relatives. The work of the physiologist frequently involves the question of relationship, as does that also of the ecologist. Indeed, every biological field is in very close connection with taxonomy.

This intimate relation is not one-sided, for each of the phases of biology contributes to a knowledge of classification. Distribution and fossil forms supply information where morphology fails, or may refute conclusions based on morphology alone. Physiological facts must be taken into account in explaining the formation of species. Ecological relations must be understood if certain taxonomic questions are to be correctly answered. In practice this close relation between taxonomy and the other phases of biology is not always observed, but all of them suffer from its neglect.

BRIEF CHARACTERIZATIONS OF THE MAJOR GROUPS OF ANIMALS

The principal groups of animals are given below with brief diagnoses which may serve as definitions. It must be understood that the characters given will often not be sufficient to distinguish all the forms in a group, for there is much variation within the groups. They are intended to give the student a general conception of the phyla, subphyla, and classes.

Phylum PROTOZOA. One-celled animals; if colonial, all cells alike.

Subphylum PLASMODROMA. Protozoa that never have cilia in any stage.

Class MASTIGOPHORA. Protozoa with flagella, which serve for locomotion or for taking food. Euglena. (Figs 31, 47, 48, 66.)

Class RHIZOPODA. Protozoa with pseudopodia or other changeable processes. Amœba. (Figs. 17, 25, 27, 64.)

Class SPOROZOA. Parasitic Protozoa, usually without motile organs or mouth, reproducing by spores. Malarial organism.

Subphylum CILIOPHORA. Protozoa having cilia in some stage.

Class CILIATA. Ciliophora with cilia throughout life. Paramecium. (Figs. 18, 65, 149, 150.)

Class SUCTORIA. Ciliophora with cilia in young stages, tentacles in adult.

Phylum PORIFERA. Diploblastic, radially symmetrical animals with body wall penetrated by numerous pores. Body usually supported by a skeleton of spicules or spongin. Sponges.

Class CALCAREA. Sponges with spicules composed of calcium carbonate, monaxon or tetraxon in form. (Figs. 67, 151, 152.)

Class HEXACTINELLIDA. Sponges with spicules composed of silicon, triaxon in form.

Class DEMOSPONGIÆ. Sponges with spicules composed of silicon, not triaxon in form, or skeleton composed of spongin, or with skeleton of both spicules and spongin.

Phylum CŒLENTERATA. Diploblastic, radially symmetrical animals with tentacles, stinging cells, single gastrovascular cavity, no anus. Two body forms are prevalent, the hydroid and the medusa. Jellyfishes, polyps, and corals.

Class HYDROZOA. Cœlenterates without stomodæum and mesenteries; sexual cells discharged to the exterior; hydroid and medusa forms in the life history of same species, or only the medusa, the latter having a velum. Polyps (including Hydra), a few corals, small jellyfishes. (Figs. 60, 61, 233, 237.)

Class SCYPHOZOA. Cœlenterates with only the medusoid, not hydroid form; velum lacking; notches at margin of umbrella. Larger jellyfishes.

Class ANTHOZOA. Cœlenterates without medusoid forms, with well-developed stomodæum and mesenteries. Sea anemones, most corals. (Fig. 70, part.)

Phylum CTENOPHORA. Triploblastic animals; symmetry partly radial, partly bilateral; eight rows of vibratile plates radially arranged. Sea walnuts or comb jellies. (Fig. 71.)

Phylum PLATYHELMINTHES. Triploblastic, bilaterally symmetrical animals with body flattened, with a single gastrovascular cavity (sometimes wanting) and no anus. Flatworms.

Class TURBELLARIA. Free-living flatworms with ciliated epidermis. Planaria. (Figs. 73, 98, 99.)

Class TREMATODA. Parasitic flatworms without cilia but with a hardened ectoderm, usually parasitic and with attaching suckers. Flukes. (Fig. 72.)

Class CESTODA. Parasitic flatworms with the body differentiated into a scolex, an enlargement usually provided with suckers and sometimes with hooks, and a chain of similar joints (proglottides), the whole being usually regarded as a colony. Tapeworms. (Fig. 74.)

Phylum NEMATHELMINTHES. Bilaterally symmetrical, triploblastic animals with an elongated cylindrical body covered with a cuticle, with a true body cavity, and a digestive tract with both mouth and anus. Roundworms. (Fig. 75.)

Phylum ECHINODERMATA. Radially symmetrical (with minor exceptions), triploblastic animals with well-developed cœlom, and usually with five antimeres,

spiny skeleton of calcareous plates, and organs of locomotion known as tube feet operated by a water-vascular system. Starfishes, sea urchins, sea cucumbers.

Class ASTEROIDEA. Free-living, typically pentamerous echinoderms with wide arms not sharply marked off from disc and with ambulacral grooves. Starfishes. (Fig. 76.)

Class OPHIUROIDEA. Free-living, typically pentamerous echinoderms with slender arms sharply marked off from disc and no ambulacral grooves. Brittle stars.

Class ECHINOIDEA. Free-living, pentamerous echinoderms without arms; test composed of calcareous plates bearing movable spines. Sea urchins, sand dollars. (Fig. 77.)

Class HOLOTHURIOIDEA. Free-living, elongated, soft-bodied echinoderms with muscular body wall and tentacles around mouth. Sea cucumbers. (Fig. 78.)

Class CRINOIDEA. Sessile echinoderms with five arms generally branched with pinnules, aboral pole usually with cirri, sometimes with jointed stalk for attachment to substratum. Feather stars, sea lilies.

Phylum ANNELIDA. Triploblastic, bilaterally symmetrical elongated animals with external and internal segmentation; cœlom usually present; setæ common. True worms. (Figs. 82, 83, 84, 100, 145, 147, 148.)

Class ARCHIANNELIDA. Marine Annelida with no setæ nor parapodia.

Class CHÆTOPODA. Annelida with setæ and a perivisceral cœlom; marine, freshwater, or terrestrial in habitat. Earthworms. (Figs. 82, 83.)

Class HIRUDINEA. Annelida without setæ, and with anterior and posterior suckers. Leeches. (Fig. 84.)

Phylum MULLUSCA. Triploblastic, bilaterally symmetrical (symmetry often obscured), unsegmented animals with a cœlom, a muscular foot and usually a shell. Mollusks.

Class AMPHINEURA. Mollusca with obvious bilateral symmetry, sometimes an eight-parted calcareous shell and several pairs of gills.

Class GASTROPODA. Mollusks with a head and with bilateral symmetry usually obscured by a spiral shell of one piece. Snails. (Fig. 79.)

Class SCAPHOPODA. Mollusca with conical tubular shell and mantle.

Class PELECYPODA. Mollusks without a head, with bilateral symmetry, a shell of two lateral valves and a mantle of two lobes. Clams, mussels. (Fig. 80.)

Class CEPHALOPODA. Mollusks with distinct bilateral symmetry and a foot bearing eyes and divided into arms usually with suckers. Cuttlefishes, octopods. (Fig. 81.)

Phylum ARTHROPODA. Triploblastic, bilaterally symmetrical, segmented animals with usually more or less dissimilar somites, a cœlom very much reduced, paired jointed appendages, and chitinous exoskeleton.

Class CRUSTACEA. Arthropods breathing by means of gills, two pairs of antennæ. Crayfishes, crabs, and shrimps. (Figs. 85, 86, 262, 263.)

Class ONYCHOPHORA. Primitive air breathing arthropods with tracheæ and nephridia. Peripatus.

Class MYRIAPODA. Arthropods with tracheæ, one pair of antennæ and many similar legs. Centipedes and millipedes. (Fig. 88.)

Class INSECTA. Arthropods with tracheæ, one pair of antennæ and three pairs of legs. Insects. (Figs. 87, 202, 257.)

Class ARACHNIDA. Arthropods with tracheæ, book lungs or book gills and no antennæ. Spiders.

Phylum CHORDATA. Animals having at some stage a skeletal axis (the notochord), gill slits in embryo or adult, and a nerve cord dorsal to the alimentary canal.

Subphylum ENTEROPNEUSTA. Worm-like chordates of somewhat doubtful systematic position.

Subphylum TUNICATA. Sac-like marine animals with a cuticular outer covering known as a tunic or test. Tunicates.

Subphylum CEPHALOCHORDA. Fish-like chordates with a permanent notochord composed of vacuolated cells. Amphioxus. (Fig. 89.)

Subphylum VERTEBRATA. Chordates in which the notochord either persists or becomes invested by cartilage, segmented, to form a vertebral column, or disappears, the vertebral column being made up of bony segments. (Figs. 118–123, 168–173.)

Class CYCLOSTOMATA. Eel-like vertebrates without functional jaws or lateral appendages. Lampreys and hagfishes.

Class ELASMOBRANCHII. Fish-like vertebrates without air bladder, with jaws, and with a cartilaginous skeleton and placoid scales. Sharks, rays, and skates. (Fig. 166.)

Class PISCES. Aquatic, cold-blooded vertebrates breathing by means of gills, with air bladder, a two-chambered heart, and usually a dermal exoskeleton of scales. Fishes. (Figs. 90, 171.)

Subclass TELEOSTOMI. Fishes with a skeleton consisting wholly or partially of bone, breathing by means of gills. True fishes. (Fig. 90.)

Subclass DIPNOI. Fishes with a skeleton of cartilage and bone, and air bladder functioning as a lung. Lungfishes.

Class AMPHIBIA. Cold-blooded vertebrates breathing by means of gills in some stage, skin usually not covered with scales, heart of three chambers. Salamanders, toads, and frogs. (Figs. 91, 92, 101, 158, 159, 163, 169, 170, 175.)

Class REPTILIA. Cold-blooded vertebrates usually covered with scales, breathing throughout life by means of lungs. Lizards, snakes, crocodilians, turtles. (Figs. 168, 249–252.)

Class AVES. Warm-blooded vertebrates with the body covered with feathers, with the fore limbs usually modified as wings, and a heart of four chambers. Birds. (Figs. 173, 266.)

Class MAMMALIA. Warm-blooded animals which are covered with hair at some stage and suckle the young, and have a diaphragm between thorax and abdomen. Mammals.

Subclass PROTOTHERIA. Egg-laying mammals. Monotremes.

Subclass METATHERIA. Pouched mammals. Marsupials. (Fig. 172.)

Subclass EUTHERIA. Viviparous mammals. True mammals. (Figs. 206, 207, 232, 253.)

Invertebrate Groups of Uncertain Position

Certain groups of invertebrates have not been assigned a definite relation to other groups. Opinion differs so widely as to their affinities that they may well be kept out of the classification for the present.

Mesozoa. Parasites apparently intermediate between the Protozoa and metazoa Not improbably degenerate relatives of the flatworms.

Nemertinea. Terrestrial, freshwater, and marine animals resembling flatworms but with a proboscis, blood-vascular system, and alimentary canal with two openings.

Nematomorpha. Long thread-like animals with the body cavity lined with epithelium, a pharyngeal nerve ring and a single ventral nerve cord.

Acanthocephala. Parasitic worms with spiny proboscis, a complex reproductive system and no alimentary canal.

Chætognatha. Marine invertebrates with a distinct cœlom, alimentary canal, nervous system and two eyes.

Rotifera. Invertebrates with a head provided with cilia, usually a cylindrical or conical body often with a shell-like covering, and a tail or foot, bifurcated at the tip where it is provided with a cement gland.

Bryozoa. Mostly colonial invertebrates resembling hydroids in form, with distinct cœlom, and with digestive tract bent in the form of a letter U. (Fig. 153.)

Phoronidea. A single genus of worm-like animals having tentacles and living in membranous tubes in the sand.

Brachiopoda. Marine tentaculate animals with a calcareous shell, composed of two unequal valves, a dorsal and a ventral.

Gephyrea. Worm-like animals of doubtful affinities.

TABULAR VIEW OF THE CLASSIFICATION OF ANIMALS AS FAR AS ORDERS

The complete classification of animals includes, of course, extinct and living forms, and there are differences of opinion as to the position and composition of many groups. The following classification, including the living and a few fossil forms, now in use in the Zoölogical Laboratory of the University of Michigan, has been compiled from many sources.

PHYLUM I. PROTOZOA

Subphylum I. Plasmodroma
- **Class I. Mastigophora**
  - Subclass I. Phytomastigina
    - Order 1. Chrysomonadina
    - Order 2. Cryptomonadina
    - Order 3. Dinoflagellata
    - Order 4. Euglenoidina
    - Order 5. Phytomonadina
  - Subclass II. Zoömastigina
    - Order 1. Protomonadina
    - Order 2. Polymastigina
    - Order 3. Hypermastigina
    - Order 4. Distomatina
    - Order 5. Cystoflagellata
- **Class II. Rhizopoda**
  - Order 1. Amœbina
  - Order 2. Rhizomastigina
  - Order 3. Heliozoa
  - Order 4. Foraminifera
  - Order 5. Radiolaria
  - Order 6. Mycetozoa
- **Class III. Sporozoa**
  - Subclass I. Telosporidia
    - Order 1. Coccidiomorpha
    - Order 2. Gregarinida
  - Subclass II. Neosporidia
    - Order 1. Cnidosporidia
    - Order 2. Sarcosporidia
    - Order 3. Haplosporidia

Subphylum II. Ciliophora
- **Class I. Ciliata**
  - Order 1. Holotricha
  - Order 2. Heterotricha
  - Order 3. Oligotricha
  - Order 4. Hypotricha
  - Order 5. Peritricha
- **Class II. Suctoria**

PHYLUM II. PORIFERA

- **Class I. Calcarea**
  - Order 1. Homocœla
  - Order 2. Heterocœla
- **Class II. Hexactinellida**
- **Class III. Demospongiæ**
  - Order 1. Tetraxonida
  - Order 2. Monaxonida
  - Order 3. Keratosa

PHYLUM III. CŒLENTERATA

- **Class I. Hydrozoa**
  - Order 1. Anthomedusæ
  - Order 2. Leptomedusæ
  - Order 3. Trachymedusæ
  - Order 4. Narcomedusæ
  - Order 5. Hydrocorallinæ
  - Order 6. Siphonophora
- **Class II. Scyphozoa**
  - Order 1. Stauromedusæ
  - Order 2. Peromedusæ
  - Order 3. Cubomedusæ
  - Order 4. Discomedusæ

PHYLUM III. CŒLENTERATA (*Continued*)

Class III. Anthozoa
- Subclass I. Alcyonaria
  - Order 1. Stolonifera
  - Order 2. Alcyonacea
  - Order 3. Gorgonacea
  - Order 4. Pennatulacea
- Subclass II. Zoantharia
  - Order 1. Edwardsiidea
  - Order 2. Actiniaria
  - Order 3. Madreporaria
  - Order 4. Zoanthidea
  - Order 5. Antipathidea
  - Order 6. Cerianthidea

PHYLUM IV. CTENOPHORA

PHYLUM V. PLATYHELMINTHES

Class I. Turbellaria
- Subclass I. Rhabdocœlida
- Subclass II. Tricladida
- Subclass III. Polycladida

Class II. Trematoda
- Subclass I. Monogenea
- Subclass II. Digenea

Class III. Cestoda

PHYLUM VI. NEMATHELMINTHES

PHYLUM VII. ECHINODERMATA

Class I. Asteroidea
Class II. Ophiuroidea
Class III. Echinoidea
Class IV. Holothurioidea
Class V. Crinoidea

PHYLUM VIII. ANNELIDA

Class I. Archiannelida
Class II. Chætopoda
- Subclass I. Polychæta
  - Order 1. Phanerocephala
  - Order 2. Cryptocephala
- Subclass II. Oligochæta
  - Order 1. Microdrili
  - Order 2. Macrodrili

Class III. Hirudinea

PHYLUM IX. MOLLUSCA

Class I. Amphineura
- Order 1. Polyplacophora
- Order 2. Aplacophora

Class II. Gastropoda
- Subclass I. Streptoneura
  - Order 1. Aspidobranchia
  - Order 2. Pectinibranchia
- Subclass II. Euthyneura
  - Order 1. Opisthobranchia
  - Order 2. Pulmonata

Class III. Scaphopoda
Class IV. Pelecypoda
- Order 1. Protobranchia
- Order 2. Filibranchia
- Order 3. Eulamellibranchia
- Order 4. Septibranchia

Class V. Cephalopoda
- Order 1. Tetrabranchia
- Order 2. Dibranchia

PHYLUM X. ARTHROPODA

Class I. Crustacea
- Subclass I. Branchiopoda
  - Order 1. Phyllopoda
  - Order 2. Cladocera
- Subclass II. Ostracoda
- Subclass III. Copepoda
- Subclass IV. Cirripedia
- Subclass V. Malacostraca
  - Order 1. Nebaliacea
  - Order 2. Anaspidacea
  - Order 3. Mysidacea
  - Order 4. Cumacea
  - Order 5. Tanaidacea
  - Order 6. Isopoda
  - Order 7. Amphipoda
  - Order 8. Euphausiacea
  - Order 9. Decapoda
  - Order 10. Stomatopoda

PHYLUM X. ARTHROPODA (*Continued*)

Class II. Onychophora
Class III. Myriapoda
- Order 1. Pauropoda
- Order 2. Diplopoda
- Order 3. Chilopoda
- Order 4. Symphyla

Class IV. Insecta
- Order 1. Aptera
- Order 2. Ephemerida
- Order 3. Odonata
- Order 4. Plecoptera
- Order 5. Isoptera
- Order 6. Corrodentia
- Order 7. Mallophaga
- Order 8. Thysanoptera
- Order 9. Euplexoptera
- Order 10. Orthoptera
- Order 11. Hemiptera
- Order 12. Neuroptera
- Order 13. Mecoptera
- Order 14. Trichoptera
- Order 15. Lepidoptera
- Order 16. Diptera
- Order 17. Siphonaptera
- Order 18. Coleoptera
- Order 19. Hymenoptera

Class V. Arachnida
- Order 1. Araneida
- Order 2. Scorpionidea
- Order 3. Phalangidea
- Order 4. Acarina
- Order 5. Pedipalpi
- Order 6. Palpigradi
- Order 7. Solifugæ
- Order 8. Chernetidia
- Order 9. Xiphosura
- Order 10. Eurypterida

GROUPS OF INVERTEBRATES OF MORE OR LESS UNCERTAIN SYSTEMATIC POSITION

- Group 1. Mesozoa
- Group 2. Nemertinea
- Group 3. Nematomorpha
- Group 4. Acanthocephala
- Group 5. Chætognatha
- Group 6. Rotifera
- Group 7. Bryozoa
- Group 8. Phoronidea
- Group 9. Brachiopoda
- Group 10. Gephyrea

PHYLUM XI. CHORDATA

Subphylum I. Enteropneusta
- Order 1. Balanoglossida
- Order 2. Cephalodiscida

Subphylum II. Tunicata
- Order 1. Ascidiacea
- Order 2. Thaliacea
- Order 3. Larvacea

Subphylum III. Cephalochorda

Subphylum IV. Vertebrata

Class I. Cyclostomata
- Subclass I. Myxinoidea
- Subclass II. Petromyzontia

Class II. Elasmobranchii
- Subclass I. Selachii
  - Order 1. Squali
  - Order 2. Raji
- Subclass II. Holocephali

Class III. Pisces
- Subclass I. Teleostomi
  - Order 1. Crossopterygii
  - Order 2. Chondrostei
  - Order 3. Holostei
  - Order 4. Teleostei
- Subclass II. Dipnoi

Class IV. Amphibia
- Order 1. Caudata
- Order 2. Salientia
- Order 3. Apoda

Class V. Reptilia
- Order 1. Testudinata
- Order 2. Rhynchocephalia
- Order 3. Crocodilini
- Order 4. Squamata

Class VI. Aves
- Subclass I. Archæornithes
- Subclass II. Neornithes
  - Order 1. Hesperornithiformes
  - Order 2. Ichthyornithiformes
  - Order 3. Struthioniformes
  - Order 4. Rheiformes
  - Order 5. Casuariiformes
  - Order 6. Crypturiformes
  - Order 7. Dinornithiformes
  - Order 8. Æpyornithiformes
  - Order 9. Apterygiformes
  - Order 10. Sphenisciformes

PHYLUM XI. CHORDATA (*Continued*)

Order 11. Colymbiformes
Order 12. Procellariiformes
Order 13. Ciconiiformes
Order 14. Anseriformes
Order 15. Falconiformes
Order 16. Galliformes
Order 17. Gruiformes
Order 18. Charadriiformes
Order 19. Cuculiformes
Order 20. Coraciiformes
Order 21. Passeriformes

Class VII. Mammalia

Subclass I. Prototheria
Order 1. Monotremata
Subclass II. Metatheria
Order 1. Marsupialia
Subclass III. Eutheria
Order 1. Insectivora
Order 2. Dermoptera
Order 3. Chiroptera
Order 4. Carnivora
Order 5. Pinnipedia
Order 6. Menotyphla
Order 7. Primates
Order 8. Rodentia
Order 9. Lagomorpha
Order 10. Artiodactyla
Order 11. Perissodactyla
Order 12. Proboscidea
Order 13. Hyracoidea
Order 14. Xenarthra
Order 15. Pholidota
Order 16. Tubulidentata
Order 17. Sirenia
Order 18. Cetacea

CHAPTER XIV

THE ANIMAL AND ITS ENVIRONMENT

Ecology embraces the study of the relations of animals and plants to the conditions in which they live. The discussion in this book has special reference to the ecological relations of animals. It has long been recognized that animals are dependent upon certain physical conditions, such as food and water, and that different forms require somewhat different conditions, for example that fishes require an aqueous medium, that some animals require plant food, and others animal food, etc. But the extent to which the peculiar combinations and intensities of the various physical and biological conditions existing in nature are necessary to the maintenance of the individuals of particular species, and to what extent the absence of these combinations and intensities may cause the destruction of the animals or influence their distribution, has but recently attracted the attention of zoölogists.

Several terms have been applied to the study of environmental relations, such as Hexiology (erroneously spelled hexicology by Mivart); Physiology of Organisms (Semper), as opposed to special physiology or physiology of organs; Bionomics (Lankester); and Oecology (Haeckel). These terms have been differently defined by different authors, but *Ecology* is now in general use and the conception that it comprises the study of all the relations of the animal to the environment seems to prevail.

Scope of Ecology.—Defined as the relation between the animal and the environment, ecology is a very broad subject and encroaches to some extent upon other fields. As so defined, it includes the relations of individuals or species to each other, such as colony formation, society formation, parasitism, slavery, symbiosis, and the relation of enemy and prey; and their relations to the physical environment, such as the effect of the chemical content and the temperature of the water, and the effect of the nature of the soil, temperature, and moisture on land.

Structural Adaptations.—The relations of animals to the environment may be classified as structural and physiological. Characters whether structural or physiological which fit an animal for life under given conditions are commonly referred to as adaptations. The most conspicuous adaptations are those of structure, including color. Thus, to take a simple example, a fish is adapted to life in the water by having fins and gills which permit it to swim and respire in that medium, while ter-

restrial mammals are adapted to life on land by having legs and lungs. Not all animals in the same environment are adapted in the same way to the conditions of that environment. Thus the manatee, whales, and porpoises, all of them aquatic mammals, do not have the fins of fishes, and they breathe by means of lungs; and many terrestrial animals do not have legs. The fact remains, however, that animals living in different conditions are often structurally different, and these differences in structure may fit them for life in their respective environments. This does not mean that all differences in structure are adaptive, for such universal adaptation has not been established; but it is reasonably clear that animals are often structurally adapted to particular conditions, and are probably never found in conditions to which their structural characters are seriously ill-adapted. As more detailed examples of structural adaptations may be mentioned the suctorial disks on the toes of the tree-inhabiting frogs, the webbed or lobate feet of ducks and other aquatic birds, the tuberculate teeth of browsing animals like the elk, and the teeth with flat grinding surfaces in grazing animals like the bison.

Animals may also be apparently adapted to particular enivironments by their coloration. Whatever the explanation may be, many forms in a particular environment have a coloration which tends to conceal them by making them look like something in the environment. However, the dependence of forms so colored upon their resemblance to specific things in the environment has not been shown, and the resemblance may be much less adaptive than commonly supposed.

Physiological Adaptation.—The general physiological dependence of animals upon the physical conditions which surround them has also long been recognized, but the extent of this dependence and the difference in the effect of the same conditions upon different forms is only now coming to be appreciated. It is generally known for example that most of the marine animals cannot live in fresh water, nor freshwater species in salt water; that many northern animals are adversely affected by the higher temperatures of the tropics, while many tropical animals cannot be acclimated to temperatures which prevail in northern latitudes; that species which thrive in regions of moist conditions many times cannot live in desert areas; and so on. It is not, however, so generally known that the dependence upon certain conditions is so close as to cause differences in the local occurrence of a form in a very limited region and in the purely local distribution of nearly related species. The data show that the physiology of the animal is affected by many conditions of the environment, and that variations in any of the conditions may be measured from an optimum (most favorable condition) which may be quite different for different species. Thus Shelford has shown that the alkalinity or acidity of the water is one of the factors governing the movement and distribution of fishes. Most fishes, when given a choice.

enter and remain in water that is slightly or distinctly alkaline, but the degree of alkalinity that appears to be best is different in different species. Temperature is another factor to which animals are physiologically adapted in different ways. Each species has its own peculiar range of temperature within which it can live or remain active, and included in this range is a more restricted one in which its growth, activity and reproduction are most favored. The adult cotton boll weevil for example, is active between 13 and 35°C., while high temperatures, from 50 to 60°C. in different specimens, and low temperatures from −4 down to −14°C. prove fatal to it. The minimum or death temperature for the honeybee is about −1.5°C., that of the house fly about −5°C. For animals that spend all or part of their life history in the ground, the structure of the soil is a factor of physiological importance. Of this factor Folsom writes as follows: "In a loose soil white grubs or wireworms go easily and rapidly from one plant to another. Tiger beetles and ants need soil of a consistence which will maintain the burrows after they are made. Caterpillars, grubs, etc., about to pupate, cannot burrow in soil that is too hard, and frequently avoid also soil that is too loose. The bollworm if unable to dig into hard baked soil will enter cracks in the soil. Some grasshoppers, on the other hand, prefer hard-packed soil in which to lay their eggs." Pressure is a factor to which aquatic animals are subjected to very different degrees. Thus, certain fishes live in deep water under a pressure that would kill shallow water forms; and when these bottom fishes are brought into shallow water or into the air they burst. The range of depths in which fishes may live varies greatly, however, in different species. The salt content of water is of considerable importance to some species, less important in others. Thus Semper states that one species of Neritina (snails) can live equally well in fresh, brackish, or sea water, while other species live only in one or the other and cannot endure any appreciable increase or decrease in the salinity. He also is authority for the statement that the stickleback, *Gasterosteus aculeatus* (a freshwater fish), will live in sea water if given food, while the freshwater clams Unio and Anodonta will perish in sea water, sometimes in a few hours. The change in alkalinity may in some cases be made also in the opposite direction without injury, for the smelt (a fish) which is principally marine will thrive in fresh water and has been introduced into many freshwater lakes. These are only a few of the physical conditions to which animals are related in a physiological way and which affect their distribution. Humidity, barometric pressure, light, water currents, and many other conditions are known to affect life processes.

Adaptation Not Purposeful.—In concluding this discussion of the nature of the relations between animals and the environment it should be noted that in referring to the structural and physiological characters

of species which fit them for life under certain conditions as adaptations, it is not understood that the relationship is purposeful. The term is now most generally used to mean the *fact* of fitness, that is, it does not refer to the *cause*. Adaptation is advantageous, but not designed. Perhaps the term adjustment would be preferable to adaptation.

Ecological Relations.—The ways in which organisms are related to their environment are exceedingly varied. Animals may be influenced by their living environment, or by the inanimate features of their surroundings. Ecological relations may exist between similar animals, between totally different ones or between animals and plants. Such relations may involve only two species, or many species. They may be highly specialized relations or somewhat incidental, and may involve benefits or disadvantages, or neither. Some of the more common ecological relations are discussed in the following pages.

Colonies.—Colony formation has been considered in the chapter on the origin of the metazoa, and it is not necessary to repeat here. An animal colony is a union of numerous individual animals by an organic body connection. True colony formation results, as pointed out in Chap. V, only from the adherence of individuals produced by fission or budding. It is not accomplished by the coalescence of originally separate individuals; the fusion of separate cells of the slime molds (Myxomycetes) into a multinucleate streaming mass (the plasmodium), and the secondary union of two individuals of a metazoön, *Diplozoön paradoxum*, in a permanent copulation, are not to be thought of as producing colonies. The marine hydroids and corals are examples of colony formation by incomplete division and budding. The colonies formed by budding may consist of thousands of individuals which have sprung from a sexually produced ancestor. Frequently in such colonies there is polymorphism, permitting the functions of the entire aggregation to be distributed among the individuals, so that there are reproductive units, units which capture and digest food, protective and sensitive units, etc.

Societies.—In social animals the reciprocal dependence of the individuals is much less than in colonial forms in that there is communal life but no organic connection. It is probable that the sexual impulse plays an important part in the formation of animal societies. It is known that under the influence of the sexual impulse many animals are drawn together temporarily; for example, sea urchins, many fishes, and snakes congregate in numbers during the breeding season. Other forms are drawn together into loose but more persistent groups apparently principally because of the reproductive impulse and for the protection of the young; herds of gregarious mammals, like the bison and deer, are examples.

Finally there are very elaborate societies among insects, in which there is pronounced division of labor and polymorphism and thus recipro-

cal dependence. Many of the ants and bees live in complex communities composed of males and females (drones and queens) and others with degenerate female sexual organs (workers). The sexual forms give rise to the next generation, while the workers care for the home, provide the food, and serve for defence. Sometimes the workers are also divided into castes with a division of labor, a common division being that between true workers and soldiers, the defence of the colony being delegated to the latter.

Parasitism.—Individuals of different species often stand in close relation to each other because of advantages which they derive from one another or because of something which one furnishes to another. Where one form attaches itself to another and derives all the benefit, the association is called *parasitism*. A *parasite* is an animal which finds its dwelling-place upon or in the body of another animal, the *host*, and obtains nourishment from it. Examples of this relationship are found among the flatworms (especially the tapeworms), the roundworms, in many insects, and less frequently in other groups. Many of these parasites are of great economic importance. Parasitic forms have come into a more or less dependent condition and many of them have undergone such extensive changes in their organization as to make them incapable of life elsewhere than on or in the host. Some biologists have supposed that these changes, many of them of a degenerative nature, have been induced directly by the parasitic mode of life. It is not improbable, however, that parasitism exercises only a selective influence upon structure, and does not initiate any changes. That is, modifications arise in the same way as other evolutionary steps, the causes of which are discussed in a later chapter, and those changes which are useful, or are not inimical, to the parasitic habit already adopted are allowed to accumulate. Some of these changes may thus lead to degeneration of structures formerly well developed.

There are two classes of parasites, those living within the host, *entoparasites*, and those living on the outside of the body, *ectoparasites*. Examples of entoparasites are tapeworms, which live in the alimentary canal, and liver flukes, which occur in the liver; and among the ectoparasites may be mentioned lice, fleas, and mites.

Symbiosis.—If the individuals of different species stand in close reciprocal relation the association is known as *symbiosis* and the associated animals are called *symbiotes*. If symbiosis is interpreted, as is done by some biologists, to mean that the species cannot exist independently, well-established cases of it are rare. A beetle of the genus Claviger is a guest in ant nests. As it is blind and cannot feed itself it must be fed by the ants, and in return it probably provides a food for the ants, since at the base of each wing cover it has a tuft of hairs which the ants lick. Other ant guests which are never found outside of the nest are

apparently fed and in return provide food for the ants in the form of secretions; others apparently clean the nests and in return are allowed to lead a protected life in the nest.

Certain species at least occasionally form partnerships which are of mutual advantage. A classic example is that of the hermit crab, *Eupagurus pubescens*, and an actinian, *Epizoanthus americanus*. The crab inhabits a snail shell, upon which the actinian rests. The latter grows until it covers the shell, or even becomes larger. It may dissolve away the shell, but the base of its body serves as a protection to the crab, and may grow sufficiently so that the crab need not seek a new shell at intervals. The advantage to the actinian is that it seizes floating particles of the food which the crab tears to pieces.

Many other cases of at least occasional relations of mutual benefit are known. "The Crocodile Bird (*Pluvianus ægyptius*) removes leeches, and perhaps fragments of food that would otherwise decay, from the mouth of the Crocodile, which, with its jaws open, permits the search" (Borradaile). The North American cowbird (*Molothrus ater*) by feeding on the backs of cattle removes parasites and receives food in return. Such relationships as the ones mentioned grade almost imperceptibly into those in which only one form receives benefit, a relationship which has been given the name *synœcy*. Thus, the remora, a fish, attaches itself to sharks and feeds on fragments of the food of the larger form. The large tropical sea anemones are said to harbour certain crustaceans and small fishes within their gastrovascular cavities.

Slavery.—Closely related to symbiosis is slavery. Social animals frequently not only hold other animals in bondage, but also protect and serve them. Domestic animals may be regarded as examples. Certain ants use the secretion of plant lice, and some of the species protect the plant lice in various ways. Because of the mutual advantages in the relation of ants and plant lice, this relation is often called symbiosis rather than slavery. Some ants enslave ants of other species which gather food or even feed their captors. The dependence in the latter case may be close, some of the slave-makers not being able to feed themselves.

Predaceous Habit.—Many animals are entirely carnivorous and many which have herbivorous habits are also flesh-eaters. Flesh-eating forms are frequently restricted in their diet, or at least feed principally upon a limited variety of animals. Thus there are *insectivores*, or insect-eaters (for example, many lizards which feed largely or exclusively upon insects); true *carnivores*, or flesh-eaters (as the dogs, which feed upon vertebrates); *piscivores*, or fish-eaters (the fishes whose main diet is fish); and so on. There is much variation in the diet of such predators, but the fact that many forms live exclusively upon animals and that many others must have animal food of a certain kind as well as plant food is an ecological relation of importance.

Mimicry.—Close superficial resemblance between two species not nearly related to one another has been termed *mimicry*. It has been noted that in the same region with certain animals, known or supposed to have exceptional means of defence, are other forms without such means of defence which resemble them very closely. For example, in southern United States the venomous coral snake occurs in the same region as a harmless snake, *Cemophora coccinea*, which resembles it so closely that the two species cannot be distinguished at a little distance, unless it is known that in the color pattern of alternating rings of red, black, and yellow there is a different sequence of colors in the two forms. The similarity is not due to common ancestry, since the two species are not closely akin. Other examples are syrphid flies which mimic wasps, and numerous cases among the butterflies. The resemblance is often very close, and may involve both form and color. In some cases one of the two forms has, and in others is popularly supposed to have, some repellent or dangerous property which saves it from attack. The repellent form is regarded as the *model*, the harmless or defenceless species as the *mimic*.

According to a theory long current, the ancestors of the two species were not similar. By natural variations some individuals of the harmless form, according to this old theory, came to possess some characteristic making them resemble slightly the distasteful species. Predatory animals, learning by experience to avoid the obnoxious animals, were deceived by the similiarity and spared the most similar members of the harmless species. The latter were supposed to survive in greater proportion than others, and to transmit their peculiarity. Continued accumulation of modifications that deceived predatory animals, so the popular explanation goes, caused the two groups to become more and more alike. This explanation can hardly be correct, however, in certain instances in which the resembling species do not live in the same region, since in these cases the predatory animals which learned by experience the disagreeable feature of the one species would not be in a position to be deceived by the harmless one. Nor could the popular theory explain the similarity of two noxious forms, instances of which are known. These latter cases of resemblance must be purely fortuitous; and since it is necessary to explain them as accidental, it is not improbable that most, perhaps all, other close resemblances between species not closely related are likewise due to chance.

Ecological Value of Species Relations.—It is clear that when the relationship between animals of different species is such that one is dependent upon the other, that relationship becomes a factor in determining the distribution. This is best exemplified by the parasitic forms. If the host is debarred from or exterminated from a certain habitat the parasite is also debarred or exterminated because of its dependence upon

the animal with which it is associated. The same is true of symbiotes; and when prey is not to be found in a region a carnivorous form is likely to be excluded from it. At this point ecology merges into the field of zoögeography. With restricted application the interrelation in habits between species is a factor in the formation of animal communities or associations as well as in the determination of geographic ranges.

Plants as Food.—Perhaps the most obvious relation between the plants and animals in a region is that which exists between plant-eaters, the *herbivores*, and their food supply. Sometimes this relationship is very close, the animal being dependent upon a certain plant for food. Many insects are thus limited in the food which they take. The larva of the butterfly *Papilio philenor* feeds on only one plant, the Dutchman's pipe; and the water beetle *Donacia piscatrix* is found almost exclusively on the yellow water lily (rarely on the white water lily). In other cases a particular kind of food furnished by various plants may be required. Thus there are browsing animals which feed upon twigs and shoots of trees and bushes, grazing animals which eat grasses and similar plants, bark-feeders, flower-feeders, mushroom-feeders, etc. For herbivorous forms with a restricted diet the nature of the vegetation is an environmental factor.

Plants as Protection.—The vegetation may also be an environmental condition in other ways. Animals which require shade, *e.g.*, some tree frogs, find favorable conditions in the forest. Some animals breed only in trees; for example, a beetle, *Buprestis nuttalli consularis*, breeds only in the decayed wood of one species of pine, *Pinus rigida*. Other forms are structurally adapted to life in trees, as the flying squirrel, and the sloth (see frontispiece) which cannot walk except when suspended from a limb. Associations held together by various kinds of dependence upon vegetation may be easily pointed out. Thus the prairie faunas are composed of many grass-eating ground forms, while the forest areas are inhabited by browsing or other types which feed upon or breed or live in trees.

Gall-forming insects usually derive both food and protection from the plants they inhabit. Some stage of the insect, most often the larva, lives in or on the tissue of the host plant and in some way stimulates the develpment of galls in which the insects are enclosed. This relation is often a very special one, since certain insects produce galls only on the hickory, some only on oak, some only on goldenrod, some only on the rose, and so on. In those cases in which two or more species form galls on the same species of plant, or in which galls are produced on plants used in some other way by another species of animal, the gall-producing habit leads to the formation of animal communities.

Highly Specialized Relations of Animals to Plants.—A few instances of the relations between animals and the plants that serve as their food

and perhaps protection are so intimate and mutually so advantageous as to require special mention. These relations are quite as close, in the examples to be described, as is the relation called symbiosis; but the term symbiosis is ordinarily applied only to relations between animals or between plants. The interdependence in these cases is, indeed, so specialized that it does not lead to the formation of animal associations, for in each instance only one species is thus related to a given plant.

Moths and Yucca.—Moths of the species *Pronuba yuccasella* live upon the developing seeds of common yuccas, and the success of the moths depends on a plentiful supply of these seeds. Now, seeds in plants develop only when the stigmas of the flowers are pollinated. The moths appear deliberately to collect the pollen from the flowers and apply it copiously to the stigmas, insuring the production of the maximum number of seeds. At the same time they lay eggs in the ovaries of the plant where the seeds later develop. There are always more seeds than are required as food for the moth larvæ, so that subsequent generations of the food plant are provided. Since the adult moth does not itself use for food the pollen which it collects, the habit of gathering it and placing it upon the stigmas has reference only to the success of the offspring. Since one cannot ascribe forethought to the adult moths in this case, their behavior is said to be instinctive; but the psychology of such remarkable behavior has never been satisfactorily explained.

Insects and Figs.—A fig is a thick-walled hollow receptacle on the inner surface of which numerous minute flowers are produced. The fig does not attain its maximum size or best flavor unless these flowers are pollinated so that seeds are produced, and pollination is wholly dependent upon an insect, the fig wasp, Blastophaga. These insects enter the fig at a minute opening in the end, for the purpose of laying their eggs, and incidentally they carry pollen from some fig previously visited. The cultivated Smyrna fig is so constructed that the eggs of Blastophaga cannot be laid in it, but the insects visit it in search of a suitable place, so that the Smyrna fig receives the benefit of pollination without offering much in return. The insects must come from inferior wild figs in which their eggs can be laid, and it is the practice of fig-growers to hang wild figs containing Blastophaga ready to emerge in the Smyrna fig-trees when the flowers of the latter are ready for pollination.

Animal Communities.—The relations of animals to their environment, discussed in the foregoing sections, are such as to bring about the formation of animal communities. The intensities of such features as temperature, salinity, moisture, and alkalinity are grouped in a general way in nature. Different degrees of these conditions are characteristic of different localities. Thus in lakes there are different conditions of temperature, gases, bottom, light, etc., at different depths; and on land the soil conditions, temperature, moisture, and other factors are different in swamps, grassland areas, and forests. Likewise there

are differences in the structural and physiological features af animals; but among these differences are many similarities, so that many animals respond in a similar way to a given environment. When environments are classified, therefore, with respect to their similarities, it is found that the animals in them fall roughly into a similar classification with respect to their responses to the environment. In this manner animal communities are established. For example, there are deep-water fishes in the inland lakes of Michigan (such as the lake trout and cisco), and whenever proper conditions are present these forms are to be found. Similarly, swamps, prairies, wooded areas, etc., over any region are characterized in general by the same animal forms in each case. Along with the characteristic animals occur other more tolerant species which live in two or more associations, but these are not so numerous as to obscure the distinctions between communities.

The classification of animal communities has not been well worked out. So far it has been based principally upon the classification of plant communities. The classification used for plants will probably continue to be used as a basis, for the plants are an important factor in the environment of the animal. One scheme of classification in use at the present time is that of Livingstone and Shreve, which is partly described as follows: "The extensive areas such as the sagebrush plains of the Great Basin, the grasslands of Nebraska and Kansas, or the pine forests of the Atlantic Coastal Plain are designated as formations. The smaller and less markedly differentiated areas within a formation are designated as associations, as, for example, the forests of shortleaf pine in New Jersey, those of loblolly pine in Maryland and Virginia, and those of longleaf pine in the Gulf States, all lying within the Coastal Plain formation. The smallest units of vegetation are (sometimes) termed societies, and those are of small area and represent portions of the association in which a definite aggregation of species is to be found." As an example of the nature and distribution of the recognized formations, a synopsis of the communties adopted by a committee of the Ecological Society of America is given below.

I. Land Communities.

(*a*) *Forests with broad thin leaves.*

1. Continuously moist and evergreen.
   (*a*) Uniformly warm, affording habitats in six or more strata. (Tropical rain forests.)
2. Intermittently dry or cold, and deciduous.
   (*a*) Warm with distinct dry season. (Tropical deciduous forest.)
   (*b*) With cold winter, little winter shelter. (Temperate deciduous forest.)

(*b*) *Communities of evergreen forests of narrow, thick leaves*

1. Moist conifer forest with little undergrowth.
2. Rainy conifer forest with shrub undergrowth.
3. Open, arid, conifer forest.

(*c*) *Communities of savanna and grassland.*
1. Tropical savanna (dry season) affording habitats in groves, thickets, forest margins, and grasslands.
2. Tropical steppe; large herds of mammals.
3. Temperate savanna; habitats in groves, thickets, forest margins, and grasslands.
4. Temperate steppe with cold or dry winters and usually large herds of mammals.
5. Arid, broken, bush-covered steppe with small herds of mammals.

(*d*) *Communities of winter rain* (forests with broad, thick leaves), *e.g.*, California semi-desert.

(*e*) *Communities of desert and semi-desert.*
1. Grass, cactus, tree semi-desert with grazing mammals (*e.g.*, South Texas semi-desert); succulent semi-desert; shrub-covered semi-desert.
2. Extreme desert without large diurnal mammals.

(*f*) *Arctic and Alpine lands.*
1. Tundra.
2. Alpine meadows.
3. Ice fields.

II. Communities of Waters and Shores.

(*a*) *Communities of the sea* (*Marine*).
1. Communities of the open sea (Pelagic).
   (*a*) Mid-oceanic communities.
   (*b*) Oceanic island communities.
   (*c*) Sargassum communities.
   (*d*) Coastal oceanic communities.
2. Communities of the sea bottom (Benthic)
3. Littoral communities.
   (*a*) Communities of eroding shores; subdivisions based on exposure, bottom material, and latitude.
   (*b*) Communities of depositing shores; subdivisions as above plus vegetation.
   (*c*) Special communities: coral; tidepools; kelp.

III. Communities of the Sea Shores. Animals feeding in the sea and breeding on the land, or vice versa. Classification based on climate.

IV. Communities of the Fresh Waters.

(*a*) *Communities of still waters.* Subdivisions based on size, depth, and vegetation: littoral, pelagic, benthic.

(*b*) *Communities of turbulent waters.* Subdivisions based on character of water movement.

(*c*) Swamps, marshes, etc.

It is not to be inferred that physiological dependence upon or preference for certain physical conditions is the only relation which has brought about the above listed associations, for some animals are there because others are, or because of the presence of certain plants. However, the fact that the associations correspond in distribution to the physical conditions indicates that the relations between the animals and the physical conditions are in considerable part responsible for them. It has been demonstrated by physiologists that animals react differently to different

stimuli, that a variation from the optimum in any one of the physical conditions essential to life constitutes a stimulus, and that the optimum may differ with different species. This has led to the conclusion that organisms differ in the nature of their protoplasm as well as in their structure and gives a basis for the interpretation of the phenomena of animal associations. The power of spontaneous movement makes it possible within certain limits for a species to find preferred conditions; animals with the same general physiological requirements drift together; and an animal community, based at least in part upon physiological dependence upon the physical environmental conditions, results.

Summary of Ecological Relations.—As was pointed out earlier, the ecological relations of animals are of many different kinds. The variations concern the number and kinds of species involved; whether it is the physical environment or other animals or plants that are concerned; whether the relations are beneficial, harmful, or neutral; and whether the relation is based on unusual structure or habit, or upon features common to many animals. It is difficult to reduce these relations to any system, yet it will be observed that they fall into the following general categories:

1. Relations between individuals of the same species.
   (*a*) Colony formation.
   (*b*) Society formation.
2. Relations between individuals of different species.
   (*a*) Parasitism.
   (*b*) Symbiosis.
   (*c*) Slavery.
   (*d*) Enemy and prey
   (*e*) Mimicry.
3. Relations of animals to the plant environment
   (*a*) Plants depended upon for food.
   (*b*) Plants depended upon for shelter, shade, etc.
4. Relations between animals and the physical environment.

Animal Reactions and Habitat.—The reference made in the preceding paragraph to preferred conditions and physiological requirements, as factors in the choice of habitats and hence in the formation of animal associations, may easily prove misleading unless restricted in its application. In higher animals, those with some degree of intelligence, there may be such things as preferred conditions. Such animals may actually seek places where their physiological requirements may be met, as a squirrel seeks the trees where nuts may be found. But there is a host of animals, low in the scale of development, which can hardly be said to have a *preference*. They do have definite physiological requirements, about which however they probably know nothing. They are found in places where these requirements are satisfied, but they did not seek those places. Sometimes, no doubt, they come upon these habitats by chance. In many cases, however, simple animals are led to particular

localities through the inexorable operations of their own responses to stimuli. These reactions are so important as to require further discussion.

Organisms, whether animals or plants, whatever their degree of organization, respond to various sorts of stimuli. These stimuli are light, temperature, gravity, galvanic current, contact, chemical substances, and so on. The character of the response to one or more stimuli is usually definite for a given species but may differ for different species. Without too much refinement of terms, any reaction of an animal in response to a stimulus is called a *tropism*, derived from a Greek word meaning "to turn." If the reaction is toward the stimulus it is said to be positive, if away it is negative. Responses to stimuli are named in accordance with the kind of stimulus applied. Thus a response to gravity is called *geotropism;* to light, *phototropism;* to temperature, *thermotropism;* to electric current, *galvanotropism;* to contact, *thigmotropism;* to chemicals, *chemotropism;* to water, *hydrotropism;* and so the list might be extended. In place of the word tropism the word *taxis* in combination with a word denoting the character of the stimulus is sometimes used, thus, *geotaxis*, *phototaxis*, *galvanotaxis*, *thigmotaxis*, and so on. The word taxis is from a Greek word meaning "to arrange," hence geotaxis means a certain arrangement of an organism's body with reference to stimulation by gravity. The modifying words positive and negative are used as before stated.

Why an animal responds in a certain way to a definite stimulus has not been determined. The fact of the response, however, and the character of the response are not matters of question since these facts can be determined experimentally under controlled conditions. Given a certain set of conditions. the organism reacts in a certain way, not because it has the power of choice but because it cannot behave in any other way. Within the organism is a responsive mechanism which operates only in a certain manner. One animal turns toward the light while an individual of another species turns from the light. The same animal may respond differently to light, depending on the other conditions that prevail; but under the same conditions the response is invariable. Each animal responds in its particular way because it cannot do otherwise.

Reaction of Lernæopoda.—How these reactions determine the relation of an organism to its habitat may be illustrated by a summary of Fasten's account of *Lernæopoda edwardsii*, a copepod parasitic on the gills of the brook trout, *Salvelinus fontinalis*, in Wisconsin and elsewhere. This parasitic copepod hatches from the egg as a free-swimming larval form which immediately by swimming with a darting spiral motion begins a search (?) for a proper host. Its body has a high specific gravity, hence it tends to settle to the bottom when the animal is not actively

swimming. In strong light, sunlight or artificial, the copepod swims near the surface of the water or toward the light, because it is positively heliotropic. To weak light its reaction is less marked, and if the light is very weak, as at night, the copepod gives no reaction at all and because of its high specific gravity it sinks to the bottom. Its behavior to light is not interfered with by most of the chemical substances used in experiments; but if into a dish containing larval copepods, the freshly excised gills of the brook trout are placed, the copepods dart about as if they sensed something in the water. If they come in contact with the gills they attach themselves at once. If in place of the gills of brook trout, gills of rainbow trout are substituted the copepods do not attach. The latter effect is also obtained if gills of German brown trout are used. Evidently something diffuses from the gills of the brook trout which does not come from the other species of trout mentioned. This must be a chemical substance. Observations on fish from the ponds show that only brook trout are infested by this parasite while the two other species of trout mentioned, as well as suckers and perch, are immune. The copepod gives a positive chemotactic response to the gills of the brook trout and not to the other fish.

Now, in the ponds during the daytime, the parasitic copepod swims near the surface in response to light; so also do the young trout, probably in response to light stimulus but also because of the presence of food organisms which likewise are positively heliotropic. At night the trout seek the bottom; and the parasite, because it does not respond to weak light and because of its specific gravity, likewise goes to the bottom. Again parasite and host are brought into close quarters. While this proximity of parasite and host is advantageous to the parasite, it is not deliberately sought. It is the animals' responses to certain stimuli which bring this parasite into relation with its animal enivironment.

Numerous other examples in support of the general conclusion that responses to stimuli determine the habitat or immediate environment of animals might readily be found. Sometimes these responses lead the animal to an advantageous situation, and may then be described as adaptive. Often, on the contrary, the reaction appears to be of no benefit whatever. The response cannot, however, lead to very harmful conditions, for the animals would then perish. Probably, in the evolution of animals, such ill-designed reactions have repeatedly originated; but if they did, their possessors perished, and we have left today only those whose reactions are useful, or neutral, or at most only slightly detrimental.

The Environment as a Whole.—The relations of animals to each other and to the physical environment have been considered separately, but it should be pointed out that it is the sum total of the physical and biological conditions affecting the life of an animal which make up the environ-

ment as a whole. The specific complex preferred by a species constitutes its habitat, and a change in any detail may determine the existence, abundance, and distribution of the form. The physical conditions, the plants, and the associated animals comprise a complex of environmental conditions so closely interrelated that variations in any feature may disturb the balance and render difficult or impossible the existence of a particular form. In this connection it should be stated that the physical conditions everywhere are changing and that the environments are thus unstable. Modern geography teaches that streams change with age in respect to the nature of the bottom, swiftness, etc., that the lakes tend to become converted into dry land, and that land may be elevated and subsequently lowered by erosion with consequent changes in soil, climatic conditions, etc. The geographical changes bring about changes in animal life; and since they are orderly a rather definite succession of associations can be shown to accompany them. For example, under normal conditions the associations in lakes come to be supplanted by those of ponds, the pond associations give place to those of marshes, and the marsh associations yield to land associations. The animal communities change in this order because this is the geographical sequence which leads to the disappearance of freshwater lakes.

Methods and Aims of Ecology.—The work of the ecologist may be defined as the determination of the animal associations and the relations of the members of each association to the environment, for the purpose of discovering the principles in accordance with which the associations are formed. In the gathering of data two groups of students have become at least partially differentiated: first, those who place chief emphasis upon the determination of associations and, second, those who pursue studies of a physiological nature, experimenting upon animals to determine the effects of varying intensities of the physical conditions which are found in the natural habitat. The differentiation among zoölogists is not as pronounced as it is in the field of plant ecology. There seems to be a growing understanding among zoloögists that while a knowledge of the associations is necessary, their composition is an end result of the reactions of the inhabitants to the features of the environment, and that the subject to yield results must concern itself with these reactions.

Ecology can hardly be considered a science comparable to morphology and embryology. It has a number of points of contact with other sciences, but it is apparently essentially intermediate between physiology and zoögeography. In so far as it concerns itself with the determination of the nature of the interrelations it is physiology, and the term physiological ecology has been used to designate this work. The results of these studies as well as the determination of the composition of the associations provide the data upon which zoögeographical studies must be based, if the latter phase of zoölogy is to be concerned with

causes. The more important questions of geographical distribution of animals, which involves to a large extent the ecological relations, are reserved for the following chapter.

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CHAPTER XV

GEOGRAPHIC DISTRIBUTION

Zoögeography is the phase of zoölogy which deals with the distribution of animals on the earth. It is sometimes spoken of as the geographical distribution of animals or as animal geography. Some of the more striking general facts regarding this distribution, and the agencies to which it must be attributed, are discussed in this chapter.

FACTS OF DISTRIBUTION

The general fact of zoögeography, that there are great differences in the distribution of animals, is obvious even to those who have not studied the subject and whose acquaintance with animals is very limited. Even to the uninitiated it is known that certain animals have a rather definite range, or region in which they are characteristically found, and that they are absent from other places. North America does not support elephants, except in captivity; the lion hunter goes to Africa; polar bears are much more common sights to the Eskimos than to men farther south; and the jungles of India maintain an animal population unlike that of the wildest regions of the new world. With the diversified data which wider experience affords, these differences of range are greatly multiplied, and may be of a wholly different nature. The facts of distribution are not in chaos, however, but may be arranged in a somewhat orderly fashion. Many of the differences in distribution may be grouped into five categories: (1) differences in the geographic position of the ranges, (2) differences in their size, (3) differences in their continuity, (4) differences in the physical conditions prevailing in them, and (5) differences in the proximity of the ranges of apparently related forms.

Differences in Geographical Position.—It is probable that with the exceptions of species related as closely as parasite and host no two kinds of animal have exactly the same range. At any rate there are great differences in geographical position. The musk ox, for example, is an arctic species; the nine-banded armadillo occurs in South America and Middle America and southern Texas; and the North American alligator is confined to the extreme southeastern part of the United States. These examples are from widely different groups. Such differences, however, are also to be found within the same group, even in groups of as low

taxonomic position as the genus. Thus the ranges of the species of the American genus Scaphiopus, the spadefoot toads, are given in a recent check list as follows: *Scaphiopus couchii*, Texas to Arizona, northern states of Mexico, Lower California; *Scaphiopus hammondii*, western and southwestern states from Montana to Texas and Mexico, and westward to the Pacific states; *Scaphiopus holbrookii holbrookii*, eastern states, Massachusetts to Florida, west to Louisiana, Texas to Arkansas; *Scaphiopus holbrookii albus*, Florida Keys and possibly the extreme southern part of the peninsula of Florida; *Scaphiopus hurterii*, Texas.

Differences in Size of Range.—Just as there are great differences in the geographical position, so there are wide differences in the size of the range occupied by different forms. The ranges of the larger taxonomic groups (families, genera) are of course more extensive than those of their subdivisions (species, varieties), when they have more than one division, because of the wide differences in the position of the ranges of the lesser groups. Thus, the range of *Gopherus polyphemus*, one of the gopher turtles, is the coast of the United States from southern South Carolina to Florida and the Mississippi River and north into southern Arkansas; the range of *Gopherus agassizii* is in the deserts of southwestern Arizona, southern Nevada, and southeastern California; and *Gopherus berlandieri* occurs in the southwestern corner of Texas and northeastern Mexico. Therefore the genus Gopherus which includes these three species has a range extending, with interruptions, from the Atlantic to the Pacific. Furthermore, the family Testudinidæ, which includes the genus Gopherus and a number of other genera, is cosmopolitan in the temperate and tropical regions except Australia and Papuasia.

There are, moreover, very great differences in the extent of the ranges of groups of the same rank, and great differences in the physical conditions inhabited by different forms. It has been stated above that the family Testudinidæ is cosmopolitan except in Australia and Papuasia. In contrast to this extensive range the family Carettochelydidæ (also turtles) is confined to the island of New Guinea, and the family Dermatemydidæ to Central America. The genus Camponotus (the carpenter ants) is found everywhere in North America (also on other continents) from the tops of the highest mountains to the lowest desert basin, from the Atlantic to the Pacific, and from the tundras of the north polar region to the tropical region along the gulf; while another genus of ants, Sympheidole, has been found only in the Garden of the Gods in Colorado.

Differences in the size of range of species may be illustrated by some of the North American species of the genus Hyla (the tree frogs). *Hyla versicolor* is found from southern Canada to the gulf states and from the Atlantic coast to Minnesota, Iowa, Arkansas and central Texas; *Hyla squirella* from Virginia to Florida, west to Texas, and northward up the

Mississippi basin to Indiana; *Hyla gratiosa* from South Carolina to Florida and Mississippi; *Hyla evittata* only along the Potomac and York rivers in Virginia and in New Jersey.

Differences in Continuity of Range.—It has long been noted that certain forms occupy a continuous area while others occur in two or more areas that may be distant from one another. Among the many examples which might be given, the following have been selected. Among the living genera in the family Camelidæ (the camels) one, Camelus (the camel and dromedary), occurs in central Asia and northern Africa; and another, Auchenia (the llama and vicuna), is found in western South America. The genus Alligator (the alligators) is composed of two species, one to be found in central China, the other in southeastern United States. These are groups comprising only a few species in each case, yet there are wide gaps in their known ranges. Perhaps more striking is the discontinuity sometimes found in the spread of a single species. Thus, the skink, *Leiolopisma laterale*, is found in the southeastern United States and in China and certain of the southern islands of the Japanese archipelago. The Central American and Mexican frog, *Leptodactylus albilabris*, occurs in the West Indies (on the Virgin Islands, Vieques, and Porto Rico) as well as on the mainland.

It is well established that discontinuous distribution occurs more frequently and is more pronounced in the larger taxonomic categories, that is, it is more common and the gaps are wider in genera than in species, in families than in genera, in orders than in families, etc. Indeed it is so rare in species as to make it a matter of doubt in most instances whether supposed discontinuity of a species range may not be due to convergent development; that is, it may be that the forms in widely separated areas which look so much alike that they are regarded as the same species are not really so closely related, but have come to resemble one another by an independent evolution towards the same goal. Discontinuity in the range of a species may also be due to transportation by man, or to accidental dispersion by nature, such as transportation to islands by means of floating vegetation.

A fact in regard to discontinuous distribution that is constantly receiving confirmation, particularly from paleontology, is that groups now interrupted in distribution were at one time continuous. Thus the presence of fossils shows that the camels, now in two or three regions separated by thousands of miles, formerly occurred more widely in Asia and also in North America; that tapirs have occurred in Europe, Asia, and North America, although now found only in the Malay Archipelago and tropical America; and that a near relative of the alligators formerly ranged widely in North America and Europe. So much evidence of this kind has been obtained that it is now generally concluded that the distribution of groups with interrupted distribution was at one time continuous, except where

accidental dispersal across barriers or dissemination by man has taken place.

Difference in Physical Conditions in Different Ranges.—The range of certain animals is in a general way coincident with areas characterized

(In far north) Treeless region of tundra and snow
Northeastern coniferous forest region.
Western coniferous forest region.
Eastern deciduous forest region.
Southeastern or coastal plain forest region.
Californian evergreen or chaparral region.
Prairie and Great Plains region.
(In southwest) Great Basin and desert region.
Tropical and sub-tropical forest region.
SCALE

FIG. 225.—General vegetation areas of North America. *(From Burlingame, Heath, Martin and Peirce's General Biology, Henry Holt and Company. Prepared by A. G. Vestal on Goode base map, University of Chicago Press.)*

by certain general physical conditions. In North America, the open, treeless areas of the west comprise the principal range of the prong-horn antelope, bison, ground squirrels, and many other forms. The eastern deciduous forest areas are inhabited by many forms that are mostly restricted to them, as the opossum, gray fox, fox squirrel, cardinal bird,

Carolina wren, and yellow-breasted chat. The coniferous forests of the north are the home of many species which extend little if any beyond them, such as the snowshoe rabbit, pine martin, northern jumping mouse, three-toed woodpecker, and spruce grouse.

The fact that within areas characterized by certain physical conditions are found animals and plants which do not extend far beyond their limits has led to the recognition of major environments (Fig 225). The conspicuous plant associations of these environments afford a convenient means of designation, and coniferous forest areas, deciduous forest areas, bunchgrass areas etc., are recognized. The environments are not sharply separated but intergrade on their common boundaries. Often this intergradation takes the form of interdigitation; that is, the regions dovetail together. The interdigitation of the plains areas of the United States with the eastern deciduous forest regions is, in its major features, shown in Fig 225, and is described by Ruthven as follows:

"It has been shown elsewhere that the prairie region cannot be merged with the forest regions of the states east of Illinois, but that neither, on the other hand, can it be classed with the arid plains. The environic conditions differ from those of the eastern forest region in being more arid and principally characterized by grass associations, and from the arid plains in being less arid and supporting a greater tree growth. Furthermore, and in harmony with these conditions, the terrestrial vertebrate fauna consists almost entirely of a mixture of eastern and western forms. In view of these conditions the region must be considered as a transition area.

"This point will not be discussed further, but it should be noted that the different elements in the fauna of northwestern Iowa occupy, as a rule, different habitats—the prairie forms being western and the marginal forest forms eastern types, while in general it is those associated with the aquatic conditions that occur in both regions. For instance, it is in the marginal forests along the shores of the streams and lakes (also now in the groves) that one finds the blue jay, Baltimore oriole, red-headed woodpecker, and many other forms characteristic of the forests of eastern North America; it is on the prairie that one finds the prairie hare, thirteen-lined spermophile, Franklin spermophile, western meadow lark, grasshopper sparrow, prairie chicken, burrowing owl and many other distinctly arid forms; while it is in the aquatic habitats that one finds the generally widely distributed water birds and amphibious mammals."

From this description it appears that the prairies are intermediate between the forest regions and the plains in the same way as a checkerboard is intermediate between a plain white board and a black one. The checkerboard is not gray, but a patchwork. While on a map of distribution typical plains animals and typical forest animals would occur together and so appear to indicate intermediate conditions, these forms tend to be distributed as an inlay or mosaic.

It is not to be inferred that more than a general uniformity in the major environments is recognizable. In each environment there are differences in rainfall, temperature, vegetation, etc., from place to place.

FIG. 226.—Annual rainfall in the lower part of the state of Michigan. This illustrates the differences in physical conditions which may prevail even in relatively small areas. (*After C. F. Schneider, Pub. 9, Mich. Geol. and Biol. Surv.*)

As an instance of this variety witness the differences in climatic conditions within the state of Michigan (Fig 226), which is in parts of two great forest areas, the deciduous and the coniferous. Furthermore, the ranges of animals are so much affected by these differences that there is

only an approximate agreement between the major environments and the characteristic forms. Certain animals extend beyond the areas and others stop short of the regional boundaries in certain directions. Many species may even have an extensive range in two or more areas. Thus,

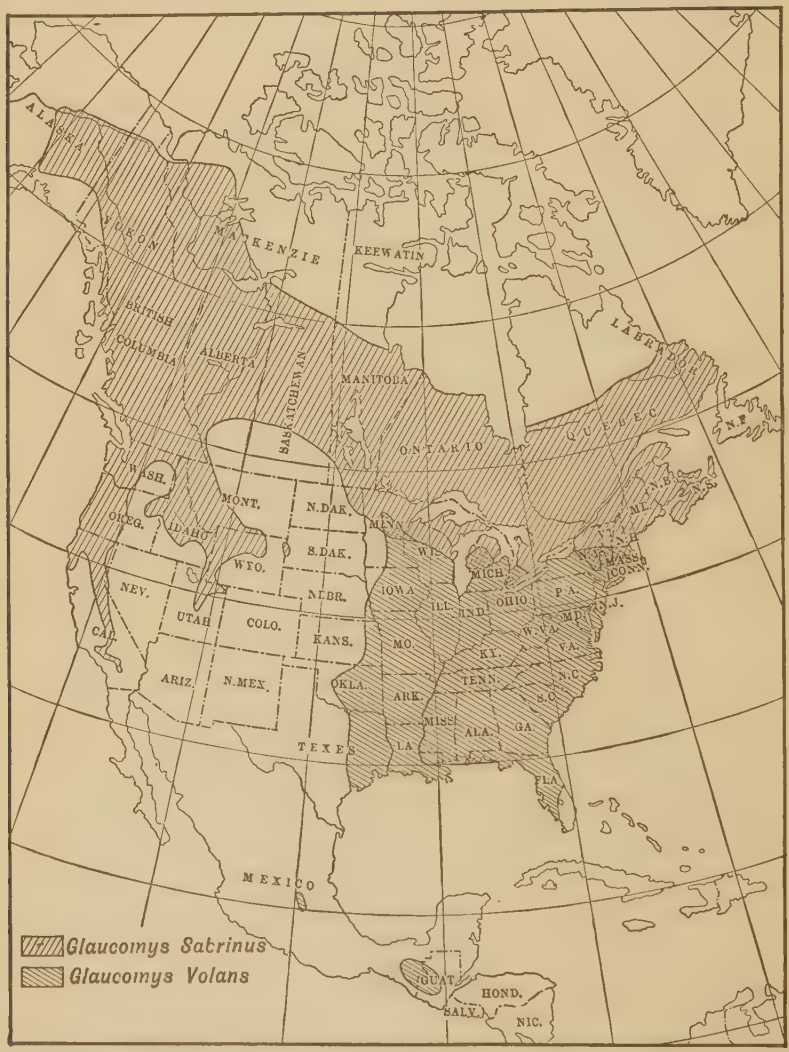

FIG. 227.—Ranges of the North American flying squirrels, *Glaucomys volans* and *G. sabrinus*. (*After Howell, North American Fauna, No.* 44.)

Rana pipiens, the common leopard frog, occurs in general over all of North America east of the Sierra Nevada Range; and the raccoon, *Procyon lotor*, frequents the deciduous forests of eastern United States and the prairie-plains region as well. If all animals showed as little relation to natural vegetation areas as do these two, the major environ-

FIG. 228.—Range of *Thamnophis sauritus proximus* (Say), the western ribbon snake. (*After Ruthven.*)

ments mentioned above would probably never have been recognized. Without pursuing this unconformity any further it may be said that there are two classes of animals which frequently ignore the major environments; first, terrestrial forms which are tolerant of a wide range of conditions, and, second, more or less aquatic forms. The leopard frog probably owes its general distribution mostly to its semiaquatic habits, and the raccoon to its tolerance.

In view of the facts (1) that the apparent major environments are occupied to a different extent by different animals, (2) that many species

FIG. 229.—Range of *Thamnophis sauritus sackeni* (Kenn.), the southeastern ribbon snake. (*After Ruthven.*)

which are chiefly confined to them transcend their limits, and (3) that many species occur over a large part of two or more regions, it may be concluded that these areas, when regarded as animal regions, are more apparent than real. They are the ranges of conspicuous plants with which are associated in certain parts some animals and plants which find there congenial conditions. These areas are not units in their biotas (animals and plants), since they mark the limits only for some of the included species, not for others. A line so drawn as to separate evergreen from deciduous trees, or two species of mammals from one another, may not separate any other two groups of organisms. It is often convenient to recognize these major environments, however, because a genus may

be divided into its component species by the regional boundaries, or the range of a species may stop on or near their limits. The range of the North American flying squirrels (Fig. 227) illustrates this correspondence with the vegetation areas. Thus the range of *Glaucomys volans* is in general the deciduous forest region and is limited to the west by the great plains, and to the north by the coniferous forests, while the range

FIG. 230.—Range of *Thamnophis sauritus* (Linnæus), the eastern ribbon snake. (*After Ruthven.*)

of *Glaucomys sabrinus* closely approximates that of the coniferous forests of the north and the mountainous regions of the west.

Differences in Proximity of Apparently Related Forms.—A conspicuous zoögeographical fact is that forms of the same group which are nearly alike are generally near together geographically. An example is found in the Sauritus group of garter snakes, several forms commonly called ribbon snakes. The ranges of these nearly related forms, *proximus* (Fig. 228), *sackeni* (Fig. 229), and *sauritus* Fig. 230) are geographically near

one another, that is, they are not separated by other forms. This proximity of the nearly related forms is diagrammatically expressed in Fig. 231. On the assumption that the relationship is a real one it has been stated that directly related forms are generally found in adjoining regions, and not in the same or distant ones. It is doubtful if this statement is always accurate, since the term region may be variously interpreted. It is safe to say, however, that while quite different forms of the same group may occur in the same or neighboring places, a form is geographically near those to which it is immediately related and more distant from those more distantly related to it.

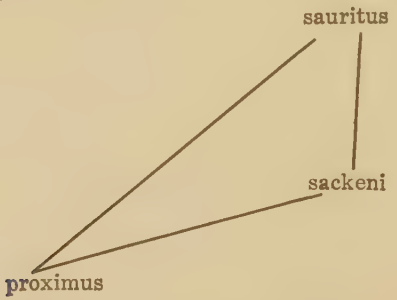

FIG. 231.—Affinities in the Sauritus group of garter snakes. It is assumed that *proximus* is the stem form and has given rise to *sackeni* and *sauritus*. The direction of evolution is *proximus*, *sackeni*, *sauritus*, or *proximus*, *sauritus*, *sackeni;* or *proximus* has given rise directly to both *sauritus* and *sackeni*. Note that if the course of evolution is *proximus*, *sauritus*, *sackeni*, it is concluded that the upper two lines indicate the direction of modification, that is the range of *sackeni* lies between those of *proximus* and *sauritus* only if the order of origin of the group is *proximus*, *sackeni*, *sauritus*. (*After Ruthven.*)

FACTORS OF DISTRIBUTION

The factors which determine the distribution of animals in nature may be inferred from the facts of distribution and the attributes of animals. A fundamental fact of zoölogy which may now be considered established is that each kind of animal has been derived from a preëxisting kind. In other words, the various groups are genetically related. Before this was established zoögeography concerned itself largely with the delineation of ranges. This is important work even now, but the ultimate goal at the present time is to determine the causes of distribution in general, the factors of distribution in specific cases, and the steps by which the present arrangement over the earth has been brought about.

Migration.—An important factor in geography is the wanderings of animals. Migration in some form or other is a fundamental attribute of animals. There are several kinds of migration, which may be termed periodic, sporadic, and normal.

Periodic Migration.—Certain forms move in large numbers from one place to another at different times of the year or at different times in their life history. The southward migration of many birds in the fall and their return in the spring is an example of seasonal migration. The

freshwater eel migrates at times separated by an interval of years. In its youth this animal ascends the rivers from the sea and lives there for years but does not breed; upon reaching maturity it returns to the sea to breed. This kind of migration may be called *periodic*, and it is doubtful whether it is effective in extending the range.

Sporadic Migration.—Somewhat allied to periodic movements perhaps are the sudden outbreaks or irruptions of a species that may occur, during which the range is widely extended. The classic example is that of the Lapland lemming, a small mammal related to the rats and mice. The migration of this species has been described by Lyell as follows. "Once or twice in a quarter of a century they appear in vast numbers, advancing along the ground and 'devouring every green thing.' Innumerable bands march from Kolen, through Northland and Finmark, to the Western Ocean, which they immediately enter; and after swimming about for some time, perish. Other bands take their route through Swedish Lapland to the Bothnian Gulf, where they are drowned in the same manner. They are followed in their journey by bears, wolves and foxes, which prey upon them incessantly. They generally move in lines, which are about three feet from each other, and exactly parallel, going directly forward through rivers and lakes; and when they meet with stacks of hay or corn gnawing their way through them instead of passing around." Another case of sudden movements is afforded by the Pallas sand grouse. This species inhabits the steppes of central Asia, extending into northern China and the Kirghiz Steppes north of the Aral Sea in the winter. At least since 1859 the bird has been in a restless and disturbed state and great waves of individuals have moved out from the normal range. In an irruption in 1859 some of them reached Poland, Holland, and the British Isles. Another outbreak in 1863 apparently involved thousands of individuals, and the birds reached Italy and the Pyrenees in the south of Europe, Scandinavia and Archangel in the north, and the British Isles and the Faroes in the west. Still another wave occurred in 1888 and at this time flocks appeared in England, Scotland, and Ireland. After each wave the species soon disappeared from the invaded countries. The extinction may have been due to slaughter by man, but while some of the invaders bred the first year they were not so well established that they could have reared young. Such sporadic outbreaks are apparently of the same nature as those which have been observed within the range of a species. A good example is the mouse plague of 1907–1908 in the Humboldt Valley, Nevada. This irruption has been described[1] as follows.

"Always present in Humboldt Valley, these mice (*Microtus montanus*) attract little attention when in small numbers. Usually they are not uniformly abundant in the district; in fact in many of the fields they may not be present at all.

[1] U. S. Dept. of Agriculture, Farmers' Bull. 352.

They live in scattered colonies in swampy places; along the borders of sloughs and irrigation ditches; in salt grass patches and in similar damp areas. When in normal numbers a little damage may be noticeable about the borders of fields or along ditches where plants have been killed during winter and spring. Ordinarily the mice are very prolific, each pair producing 4 to 6 litters of about 6 young each during the long breeding season, which extends from March to November; and probably the young born early in the season breed before fall. Occasionally conditions favor excessive multiplication, and under such circumstances damage soon becomes evident, and in a single season may increase locally to the serious injury of fields. Extending from such centers during the next breeding season, and increasing not only by reproduction but by joining with other colonies, a vast army of mice is formed. Because of overcrowding and the limitation of food, such armies invade adjoining districts, and this progress becomes more rapid with the disappearance of green food in the fall. Through the combination of several such armies, entire districts are overrun.

"Damage by field mice attracted the attention of the ranchmen in the lower part of the Humboldt Valley early in the spring of 1906 and became severe during the following summer. In the fall and winter of 1906–1907, damage had increased until fields here and there in the valley were seriously injured. Extensive ravages first occurred above and about Lovelocks. In May, 1907, fields on the Rodgers ranch, 5 miles below Lovelocks, were invaded from the lands farther up the valley, the progress of the mice being plainly marked, as the fields above the Rodgers ranch suffered first. The movement of this great body of mice, it should be noted, was a gradual, scattering progression, first by a few and later by increasing numbers, until the greater part had moved to fresh fields. Numbers, however, finding conditions improved, remained as stragglers in the fields deserted by the main body.

"By October, 1907, a large part of the cultivated lands in this district had been overrun by vast numbers of mice. The yield of hay had been reduced by one-third; potatoes and root crops were largely destroyed; many alfalfa fields were ruined by the mice eating the roots of the plants; and the complete destruction of this, the chief crop of the valley, was threatened.

"The height of abundance was reached in November, when it was estimated that on many large ranches there were from 8,000 to 12,000 mice to each acre. The fields were riddled by their holes, which were scarcely a step apart, and over large areas averaged 150 to 175 to the square rod. Ditch embankments were honeycombed, and the scene was one of devastation. Serious losses in hay and root crops during the summer proved but a slight forerunner of the damage which began in the fall with the disappearance of green food. Burrowing down about the plants, and extending their underground runs from root to root, they either killed or seriously injured the alfalfa. By November they had destroyed so large a percentage of the plants that many fields were plowed up as hopelessly ruined. They attacked also the roots of trees, seriously injuring or quite destroying orchards. They killed most of the young shade trees planted along ditches, and so completely girdled large Lombardy and silver poplars that in some cases they caused the death of even such hardy trees.

"By January, 1908, in fields where the mice had existed by thousands the previous summer and fall, comparatively few, possibly 200 to 500 to each acre,

remained. The border of the destroyed district was about 6 miles below Lovelocks, and the mice were gradually moving farther down the valley. In the area below this mice were somewhat in excess of normal numbers and in several centers of abundance had seriously injured fields. Even where most abundant, along the lower border of the affected area, they did not exceed 1,500 to the acre. In the winter they attacked every available food supply. Small willows and even greasewood bushes about the borders of fields were stripped of all the bark within reach, and horse and cattle droppings were gnawed to pieces for the food they contained. Alfalfa roots, however, were the food supply on which the mice were chiefly dependent."

Apparently *sporadic migration*, as these irruptive movements may be termed, does not usually result in an extension of range, for the species are not in the cases observed able to maintain themselves in the invaded regions. However, it is at least not impossible that at times such irruptions have brought species into regions where conditions were favorable and thus enlarged the inhabited area. Instances of widely discontinuous range have sometimes been explained, whether correctly or not, by sporadic migration.

Normal Migration.—In addition to the above types of migration, and some variations of them, every species has a kind of movement which may be called *normal migration*. This is best seen in free-moving terrestrial forms. Among the individuals of such forms there is constant movement; and either as individuals or as flocks they wander about over a larger or smaller area, according to their powers of locomotion, to seek food, escape enemies, or find mates. After the young are born they also begin to wander about in search of food, with the additional incentive of finding a new home. The individuals on the outskirts of the range thus constantly tend to invade new territory, and where not delimited by unfavorable conditions the form gradually spreads. In the absence of physical barriers the individuals of a species are held together by breeding instincts, so that each individual does not tend to wander far away from its fellows, or if it does it dies without progeny. It is for this reason that the spreading from the periphery of the range is relatively gradual. When the powers of migration and propagation are great the movement becomes more rapid. An illustration of the rapid spreading of a species is furnished by the potato beetle, *Leptinotarsa decemlineata*, whose migration has been briefly summarized by Tower as follows.

"The original distribution of *decemlineata* was on the eastern slope of the Rocky Mountains northward to the Canadian boundary, eastward into western Kansas and Nebraska, and southward into Texas and New Mexico. In this habitat it was found by Say in 1823. Then, as now, it was probably sparsely distributed over the area, feeding upon *Solanum rostratum*. I know of no record of its having been found at an elevation over 8,000 feet, or in the Great Basin.

"In this habitat it remained in stability until 1845 or 1850, when the western extension of human colonization introduced into its habitat a new factor by the

addition to the flora of a new plant which proved to be an acceptable food, *Solanum tuberosum*.

"About 1845 or 1850 the settlers in the Mississippi valley, in making their advance westward, brought the cultivated potato into the edge of the habitat of *decemlineata*, where the beetle soon learned to use it as a food. This extension of the area wherein *S. tuberosum* was grown into the habitat of *decemlineata* resulted in the removal of a previously existing barrier to further eastward extension. This barrier was the wide stretch of country in which no food plant had hitherto been available and into which it could not go without food. The advent of this new food, however, completely removed the barrier and there lay open to the eastward an expanse of territory where optimum conditions of existence were developed. Into this area it began to spread—at first slowly and in small numbers and unnoticed; then in increasing numbers and more rapidly, making itself felt as an economic factor in agriculture. Onward it advanced yearly, in increasing numbers and speed, until twenty years from its start it had reached the Atlantic coast, a barrier beyond which it has not been able to successfully pass. Fortunately the history of this advance is known from extensive records, so that it can be traced in detail from year to year."

Although the phenomenon of normal migration is most easily seen and comprehended in active terrestrial species it is an attribute of all forms whether free-moving or fixed. In fixed aquatic forms and in some slow-moving species the young are liberated as free-swimming organisms, or they become attached to free-swimming animals and thus bring about an increase in the range of the form. For example, the young of our freshwater Unios (clams) soon after escaping from the mother become attached to the gills of fishes for a period. In addition to being a general method of migration, normal migration is with little doubt the most effective means of dispersal, for it permits the species to become acclimated to new conditions encountered. It is generally slow, but when the age of the form is taken into consideration it is seen to be not too slow to account for the present range of even the slow-moving species. For example Gadow states that if a pair of earthworms are sufficient to occupy one square yard of earth per year with their offspring, their descendants long before 30,000 years (a not improbable estimate of the time since the ice age) would have choked the whole earth if not repressed. Again, if a human family moved gypsy fashion, only on one day of each week, and not more than three miles, then it would wander about 156 miles each year, and the Mongolians, crossing Behring Strait might have, at this rate, reached the Straits of Magellan in about fifty years. It is thus believed by zoögeographers that normal migration is at once the general and most effective method of extending the range and that it is sufficient to account for the size of the range of most animals.

Accidental Dispersal.—Reference to accidental dispersal has been made in the discussion of discontinuous ranges. Animals are sometimes carried on rafts or floating logs or are blown by the wind beyond their

normal range. Marine birds, such as the gannet, are occasionally, during storm, blown inland from the Atlantic Ocean, as far west as Michigan, and a number of observers in the tropics have noted terrestrial animals on floating logs and rafts in the rivers and even out at sea. It has often been asserted that this method of dispersal, which may be called *accidental*, is efficacious in extending the range. Islands may have received certain forms by accident, but there are many difficulties in accounting for the entire faunas of islands in this way. Some of these difficulties are the inability of some forms to survive a long sea voyage, the fact that many island forms, such as the giant tortoises, could not possibly be carried on rafts or blown by the winds, the necessity that in the higher animals at least a pair of individuals or a pregnant female be landed if the form is to be perpetuated, etc. But the greatest obstacle to the acceptance of accidental dispersal as an effective method of extending ranges lies in the fact that actually observed cases of accidental dissemination beyond the range of a form are very few and mostly open to question. A conservative view is that it may operate at rare intervals and for certain forms, and most often over short distances.

Distribution by Man.—Human agency is responsible for the introduction of animals and plants to new regions in a few cases that are well known, and probably in numerous cases of which we are ignorant. Introduction may have been designed, or accidental. Sometimes the forms thus introduced have flourished exceedingly in the new range, witness the rabbit in Australia, the cotton boll weevil in southern United States, and the English sparrow in America. These instances lend color to the view that many species, living with moderate success or with difficulty in regions now occupied by them, require only to be transported to other places to multiply with rapidity or even to become dominant forms. It is not improbable that species that appear to be on the road to extinction owe the reduction in their numbers either to changes in their environment or to changes in themselves, and that removal to a habitat not ordinarily accessible to them would spell the difference between destruction and rehabilitation.

Dependence upon Environmental Conditions.—Another factor of distribution is the dependence of each kind of animal upon certain conditions. This is discussed in the chapter on ecology, but it should be pointed out here that since animals are physiologically and often morphologically dependent upon certain conditions, the absence of these conditions will limit the range of the species in nature; or, as is often said, conditions other than those to which the animal is adjusted constitute a barrier to migration.

Barriers to migration are of two kinds: first, barriers that cannot be passed by means of the powers of locomotion of the animals, and second, uninhabitable areas. An expanse of salt water, such as intervenes between

islands and the mainland, is a barrier to many land animals because they cannot swim across it, while a plains area is a barrier to typical forest forms, such as flying squirrels, not because they cannot move about on the plains but because the conditions of life are so unfavorable for existence that the forms cannot spread across them. The nature and effectiveness of barriers can easily be shown to depend upon the nature of the animal. Conditions which serve as a barrier to some animals will not act as a barrier to others. Furthermore, any feature of the environment, whether temperature, moisture, size of area, soil, absence of food, vegetation, other animals, or any other condition, may be the specific cause of unfavorableness if the animal is closely dependent upon some quality or degree of that feature.

Diversity and Mutability of Environment.—Closely related to migration as a factor of distribution and to the physiological and morphological dependence of animals on specific conditions is the diversity and changeableness of the earth's surface. It is common knowledge that there are great differences in temperature between the equatorial regions on the one hand and the polar regions on the other; that there are great differences in temperature between places in the same latitudes, depending upon altitude and upon the presence of large bodies of water, ocean currents, etc.; that the amount of rainfall varies enormously, being in some places as high as 100 inches annually and in others as little as a trace for years at a time; that there are great differences in soil; that some regions have only a very scanty desert flora, others are open grass lands, and still others are covered with forests which vary in density and the species which compose them; and that the waters vary in chemical composition, depth, size, etc., in addition to temperature. In fact there are no two areas that are exactly the same in the conditions which may affect animals, and no single area, if at all extensive, is the same throughout.

The data of geology also reveal that the physical conditions on the surface of the earth are constantly being altered, and that the changes which have taken place in the past are very great (Figs. 264 and 265). Continents have been broken apart and united, islands have appeared and disappeared or been connected with and severed from the mainland, and climates have changed. Even at the present time it is evident that mountains are being destroyed, lakes filled in by débris, and the chemical nature of the water is being changed in many places. Moreover, with the constant modification which the surface of the earth has undergone and is undergoing the vegetation also has changed and is changing, as is evidenced either by a displacement of one association by another, such as a forest by a prairie, or by an alteration in the composition of the plant associations.

From what has been said concerning migration and dependence upon environments it will be readily perceived that the earth provides a multitude of environments, each of which may serve in turn as a barrier to a form in a neighboring region. A region which it has been impossible for an animal to enter may undergo such a change in some one or more of its physical or biological features that it no longer serves as a barrier. Thus the range of the potato beetle as stated above was, previously to 1850, apparently restricted on the east by the absence of a suitable food plant in the adjoining territory, but when a food plant was introduced migration in this direction began at once. Another instance, on a small scale, has recently been noted. Previously to 1907, the fox squirrel, a forest animal, was in northwestern Iowa confined to the timber along the larger streams. Since that date, owing to the number and size of the trees planted on the prairies by the residents, the squirrel has spread over large parts of the prairie areas. That changes on a much greater scale have in the past resulted in extensive changes of range seems to be shown by paleontology. Thus there is reason to believe from the relations of the faunas that Madagascar was at one time connected with Africa, South America has been joined to Australia and New Zealand, and North America and Asia have been united. Extensive migrations of animals have apparently occurred between these countries and then been halted by a breaking of the connections. Similarly the great changes in climate which occurred in North America and Europe during the Pleistocene epoch, from somewhat more equable and milder conditions than prevail at present, to polar conditions, brought the musk ox, caribou, reindeer and similar forms into the United States and Europe far south of their present ranges.

Extinction.—Complete annihilation of a species in any region is also to be regarded as a factor of distribution, though in a sense somewhat different from that in which the preceding agencies are factors of distribution. Extinction does not affect the process of distribution, but it does help determine the range occupied. Extinction of itself neither helps nor hinders the spread of animals to new regions; but the destruction of the form in some part of the area occupied by it changes the range. Distribution as a condition is thus affected by extinction; distribution as a process is not so affected.

That whole races of animals may be exterminated is very evident in the effect which man has had upon the fauna. In North America, the passenger pigeon, the Carolina parrakeet, and other species have been exterminated, other forms are on the verge of extinction, and numerous species have been greatly reduced in numbers. It is equally evident that extinction occurs in nature. The rocks and soil contain fossil remains of thousands of forms which are no longer to be found alive. There is no reason to believe that the causes of extinction in the past

were in the main different from those that prevail at present. It has been noted that diseases, droughts, exceptionally cold weather, multiplication of enemies, changes in the substances held in the water in the case of aquatic forms, increased moisture, and other agencies destroy wild animals now. Specifically it may be pointed out that during exceptionally severe winters the quail in southern Michigan become greatly depleted in numbers; that the contagious rinderpest which swept across Africa a number of years ago is said to have destroyed 65 per cent of the hoofed animals of that continent; that during winters characterized by excessive snowfall the deer in northern Michigan perish in considerable numbers because they are unable to move about freely and thus are more liable to attack by wolves; and that during exceptional droughts on the pampas of South America and Africa large numbers of wild animals die of thirst, or because, being compelled to get water at a few places, they are more readily attacked by carnivorous species. The causes of extinction are very often obscure either because they work imperceptibly or because they cannot be inferred from the remains of the animals. However, from the fact that animals are morphologically and physiologically dependent upon their environment, it may be safely concluded that just as the range is limited by environmental conditions, so any change in these conditions in the inhabited area will, if great enough, lead to extinction; and if the change is coextensive with the range total extermination of the race will result.

Evolution.—Many of the facts of distribution are capable of interpretation by the assumption that evolution has operated with the other factors. If each kind of animal has arisen from a preëxisting kind, then each group of related animals must have had an ancestral form, and if the component parts of the groups are widespread the range of the ancestral form may be considered to be the center of dispersal of the group. The facts of distribution can apparently be interpreted only on this basis.

Accepting evolution, along with the other factors which can be recognized, the method of distribution is generally conceived to be as follows. The ancestral form tends to spread in all directions. In some directions it is limited by unfavorable conditions either throughout its life or for some time. In other directions it extends its range. Anywhere within its range new types of individuals may arise through the process of evolution. These new types may be fitted to occupy new regions, and if they are formed near the limits of the range they may find opportunity to spread into areas which are inaccessible to the unaltered members of the species. Thus may arise recognizably distinct forms coincident in range with certain environmental conditions. If particular forms, or the individuals of a single form, are accidentally (or possibly by sporadic migration) transferred across barriers the distribution of the group

becomes discontinuous. If these processes have been going on for a long time, that is, if the common ancestors of a group of forms existed long ago, the range may have had time to become very extensive, or its discontinuity very marked. If, contrariwise, the ancestors were comparatively recent, the range is likely to be much smaller. For this reason, groups that have diverged far enough to have attained the rank of families are on the whole more widespread than those so nearly allied as to be considered genera. Should the environment become altered within a given range, the occupying form might be driven from it or destroyed. If the environment in a region adjoining a range should change in a favorable manner, the range might be extended at that point without any alteration on the part of the animals.

The distribution of animals is inferred to be in harmony with this method, which involves, it will be noted, the factors of migration, evolution, physiological and morphological dependence upon the environment, the diversity and changeableness of the earth's surface, and extinction; and in this manner are explained the differences in geographical position, differences in size of range, differences in the continuity of range and the fact that ranges are at first continuous, differences in physical and biological conditions which characterize the ranges of different forms, and the geographical proximity of apparently related forms.

Methods and Aims of Zoögeography.—The principal data of zoögeography are museum specimens and published records of the occurrence of the forms. Modern museums endeavor to preserve specimens with detailed locality data and to obtain material from every part of the range of each species. From the museum specimens and records (and the student must usually obtain them from as many museums as possible) the ranges are described or mapped. The descriptions are usually brief summaries in which the localities on the outskirts of the known range are given. For example Stejneger and Barbour give the range of the frog *Pseudacris ornata* as "South Carolina to Florida, west to Texas," and that of *Pseudacris feriarum* as "Eastern United States, west to Illinois." When the distribution is mapped this is usually done by plotting the known localities or by connecting the outermost locality records and covering the enclosed area with symbols or shading. At present an increasing number of museums are endeavoring to preserve ecological data, and in time it should be possible to describe the range in terms of the environmental conditions; for example Stejneger and Barbour describe the range of the small blind snake *Siagonodon humilis* as "Deserts of Arizona, southern California, Lower California and northwestern Mexico." An advantage of this method is that it permits the student to judge of the possible completeness of the data, for if the principal range of a form as indicated by the records lies within a particular environment it is more

liable to occur in parts of this environment which have not been explored than in adjacent areas having different conditions.

Many of the generalizations in zoögeography have been concerned with attempts to discover and delimit so-called natural regions. The fact that several species of animals are apparently limited in range by one factor in the environment, such as particular temperatures, and that conspicuous species of plants may have the same limitations of range has led students to attempt the delineation of areas on the basis of certain features and aggregations of forms. Thus the world has been divided into *major regions* or *realms* and the continents into smaller *provinces* or *life zones*. A critical study of these regions shows that they are principally based upon one or a few groups, for example, mammals, or mammals and birds; that students of different groups fail to agree on the extent of the regions; and that, as far the inhabitants are concerned, they are based upon averages. In other words, neither different groups nor different forms in the same group respond equally to any one feature in the environment. This is what we are led to expect from the data of ecology. It would seem to follow that since each kind of animal is adapted to certain specific conditions, though there may be certain general regions for particular groups, the search for faunal regions applicable to several groups and based on one or a few environmental factors is hopeless. Progress in interpreting the distribution of animals can be made only by working out the geographical history of each group separately, and attempting to discover the several factors which have influenced its wanderings.

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CHAPTER XVI

FOSSIL ANIMALS

Many of the fundamental problems which exist in connection with living organisms may also be studied, and in some degree solved, with reference to beings, now extinct, which lived on the earth in times past. This biology of ancient life is termed *paleontology*. Paleontology may be defined as the science of fossil organisms. When concerned with animals only, it is sometimes called *paleozoölogy* as distinguished from *paleobotany*. Anything having to do with animals not now living, and of which we have no knoweldge except that derived from their remains, is part of paleontology. The paleontologist may study structure and classification only, or he may be interested in distribution, or in modes of life and relation to environment, or in the evolution of past animals. Thus for nearly every feature of the zoölogy of modern animals there is a corresponding branch of paleontology. Many facts concerning organisms of the past can only be inferred, and there is no way in which experiment may be applied to extinct forms; but in some other respects the paleontologist has sources of information far superior to any possessed by the student of modern life.

Nature of Fossils.—A *fossil* is, literally, something dug up. As ordinarily used, the term includes any trace of prehistoric life. Fossils are usually petrifactions of parts of the animals or plants themselves, but may be any other signs of the existence of such life. The term usually implies that the parts or traces of organisms have been buried, though this feature should probably not be insisted upon. In rare instances animals have been preserved in the flesh, almost as successfully as if immersed in spirits in a museum. Large mammals have been removed from peat bogs in various parts of the world, still in a good state of preservation. Mammoths (elephant-like animals) have been buried in frozen soil in Siberia and elsewhere for thousands of years, and then recovered practically intact (Fig. 232). Oil-bearing soils in central Europe have yielded a rhinoceros and a mammoth with some of the flesh still in place. Small animals, such as insects and even lizards have been found entire in deposits of amber. This substance is of resinous nature and of uncertain origin, being perhaps derived from pine trees. At first liquid, it flowed over and embedded the small bodies without injury to them, and then hardened. Some of the most beautiful of fossil insects are of this kind.

More often only a part of an animal is represented by its fossil, and usually only the hard parts are left. In the vertebrates the bones of

FIG. 232.—Mammoth found frozen in Siberia in 1901. Most of the flesh was still on the body and intact. The skin is mounted in the museum of Leningrad in the posture in which it was found. (*From Lull's Organic Evolution, courtesy of The Macmillan Company.*)

the skeleton are commonly preserved; in insects and Crustacea, the chitinous external skeleton; in mollusks, the shell; in corals, the calcareous tubes (Fig. 233). Fleshy parts usually decompose too soon to leave

FIG. 233.—Fossil chain coral, Halysites, found in Michigan, demonstrating that Michigan was once covered with marine waters and illustrating the principle that it is the hard parts of animals that are preserved. (*From specimen in the Museum of Geology, University of Michigan.*)

an impression of their form in the hardening rock layers. Nevertheless, occasional fossilized soft animals are found; and in rare instances minute

histological details, such as the structure of the kidney and of striated muscle are observable in fossils.

The remnants which we call fossils may represent the original animals in very different ways. In some, the original structures are practically unchanged; in others they are completely replaced with minerals; and between these extremes there are various degrees of replacement. The animals, or parts of them, were buried in deposits of silt at the bottom of bodies of water, or under wind-blown material. Bones buried in dry sand in an arid region may be practically the same bones today. But bones buried in silt, which later hardened into layers of rock now far beneath the surface of the land, have been constantly subjected to the action of percolating ground water. Particle by particle they have been dissolved away, and bit by bit replaced by deposits of minerals carried in solution in the water. This replacement by minerals is known as *petrifaction*. The petrified object is not converted into minerals, it is

FIG. 234.—Diagram illustrating molds and casts. Horizontal shading represents sedimentary deposits, vertical shading the material subsequently filled in. *a*, mold of a shell which has been dissolved away by ground water; *b*, cast formed by subsequent filling in of the cavity of *a*; *c*, mold of a shell whose interior was filled with sediment; the shell itself was subsequently removed in solution; *d*, cast produced by filling the mold represented in *c*. (*From Schuchert's Historical Geology, courtesy of John Wiley & Sons, Inc.*)

merely replaced by minerals. In one fossil this replacement may have gone to completion, the original substance being entirely absent, in another the original material may be interspersed with islands of mineral deposits. In general, the older the fossil the more nearly complete is its petrifaction.

Molds are produced when the hard substance of a buried animal is dissolved away, but is not replaced by minerals. A cavity in the rock is thus formed, showing the external form of the original. This mold may be subsequently filled, forming a *cast;* but since the original was not replaced particle by particle the internal structure is not preserved. Figure 234 illustrates the relation of molds and casts to the original object. Casts may also be formed in the cavities of natural objects, such as snail shells; but here also the internal structure of the animal is not shown. Molds and casts are regarded as fossils, though no part of the original object is represented.

Animal *tracks* may also be fossilized by being filled in with later deposits of sediment. When the deposits solidify into rock, and are split

FIG. 235.—Footprints of two dinosaurs (one large and one small) and rain marks preserved in a slab of Triassic sandstone. (*From Schuchert's Historical Geology, courtesy of John Wiley & Sons, Inc.*)

apart, the lower stratum contains a mold, the upper one a cast, of the animal's foot. Figures 235 and 236 represent such a footprint. Plant

FIG. 236.—Natural casts of dinosaur tracks and rain imprints. (*From Schuchert's Historical Geology, courtesy of John Wiley & Sons, Inc.*)

impressions are likewise very common, a considerable proportion of fossil plant life consisting of molds and casts.

Subsequent Fate of Fossils.—Once a fossil is formed it is subject to physical agencies that may destroy it completely or considerably distort

it. Formed under water, the rock strata in which fossils are now being discovered were elevated and drained. In this process of elevation, folding and breaking of the rocks, many fossils were injured or destroyed. Circulating ground water may redissolve the material of which the fossils are composed; and if the material is replaced the internal structure of the animal is likely to be lost. Erosion lays bare numerous fossils, which may be weather-worn, or washed away; and if the fossils were in fragments the parts are scattered beyond recovery. Pressure in the rock strata, due in part to the weight of rock above, but perhaps more largely to shrinkage of the sediment in drying out, crushes many fossils, so that the latter are often in fragments and far from representative of the original form of the animals.

Discovery of Fossils.—Fossils are not found everywhere, and it is seldom that the paleontologist sets out to find them without some clue. Natural erosion may lay bare deposits of great value, in which the fossils are accidentally discovered by travelers or exploring parties. Excavations for buildings, drainage canals and ditches, railroad cuts, mines and quarries are prolific sources of first discoveries. Particularly valuable leads are often followed up by scientific expeditions sent out by museums and universities. Most of the valuable collections have been brought together by this concentrated, directed effort, not by casual discoveries.

Change in Species during Geological Time.—The primary fact of paleontology, which makes the study of fossils both fascinating and important, is that the animals of the past were very often unlike the animals of today. There are, it is true, many instances in which there is little or no difference between extinct and living animals, especially in late geological periods. Even in early periods some forms existed which were very similar to animals of today. Lingula, one of the brachiopods still living in marine waters, is almost identical with certain very ancient fossil brachiopods. But among the older forms of life similarity to recent forms is exceptional.

Moreover, the living beings of one past age differed from those that preceded or followed them. Examination of successively deeper and deeper strata of rock reveals differences in the animals which lived when those rocks were deposited. Animals which are abundant in the lower (older) strata are wanting in those above, while new forms take their place in the more recent rocks. So characteristic are these changes from one stratum to another that geological time may be measured, or at least divided, with reference to the fossils contained in the rocks.

In order to be able to speak of the successive rock deposits geologists employ a series of terms like those in the accompanying time scale. It is given only in its major features, and should be mastered even by the beginning student.

GEOLOGICAL TIME SCALE[1]

Eras	Major Divisions	Periods	Dominant Life
Psychozoic		Recent	Age of man
Cenozoic	Quaternary	Pleistocene (Glacial)	Age of mammals and modern floras
	Tertiary	Pliocene Miocene Oligocene Eocene	
Mesozoic		Cretaceous Comanchian Jurassic Triassic	Age of reptiles
Paleozoic	Carboniferous	Permian Pennsylvanian Mississippian	Age of amphibians and lycopods
		Devonian Silurian	Age of fishes
		Ordovician Cambrian	Age of higher (shelled) invertebrates
Proterozoic		Keweenawan Animikian Huronian	Age of primitive marine invertebrates
Archeozoic		Laurentian Keewatin	Age of supposed unicellular life

[1] The periods of a geological time scale are arranged in the same order as the strata belonging to them, that is, with the oldest at the bottom. To read such a table in chronological order one must therefore begin at the bottom.

In determining the period to which a given rock stratum belongs the character of the rock itself is usually of little value. The fossil animals and plants are used as recognition marks. Though there is some irregularity in the occurrence of some kinds of animals, certain fossils are so characteristic of a given geological age that they are termed "index fossils." It is assumed that, the world over, these animals lived at approximately the same time, and that their remains are now found in contemporaneous rocks. While this assumption is probably incorrect

in some cases, as pointed out below, it almost certainly is true as a general proposition.

The interpretations to be put upon the differences in the animals of successive periods of time are manifold. The same group of facts may often be made to bear upon a variety of questions.

Change of Environment.—Probably nothing will appeal more forcibly to a person who knows something of living animals and the habitats in which they are found, than to discover in his excursions afield a fossil animal in a region where it could not possibly exist under present conditions. In Michigan, for example, some of the finest of extinct corals are found (Figs. 233 and 237). Corals are today exclusively marine animals, and presumably were marine in earlier times. Yet Michigan is now in mid-continent, hundreds of miles from the nearest salt water. The environment has changed. This is not an isolated instance, it is but one of many similar cases. Continents and shore lines have changed often and greatly, as fossil land and marine animals testify.

FIG. 237.—Fossil cup cora found in Michigan, demonstrating that Michigan was once covered with marine waters. (*From specimen in the Museum of Geology, University of Michigan.*)

The same spot on the earth's surface has been repeatedly dry land and under water. Fossils indicate that swamps have changed to plains, forests to grasslands and finally to deserts. Climatic changes have been frequent. Tropical temperatures, as indicated by luxuriant plant growth and attendant animals, changed to winter severity, which was later ameliorated. Humid regions have become arid in many places. No other assumptions will explain the fossils found at different levels in the same region.

Migrations of Animals.—The changes in the nature of the earth's surface in the past necessitated the migration or extinction of most if not all of the animals inhabiting the changing regions. Some of these earth changes were radical. As Michigan, for example, changed from sea bottom to dry land by the elevation of the earth's crust, marine animals necessarily either followed the sea as it receded, or became modified so as to be capable of life under new conditions. Probably no animals emerged from the sea, during these changes, to live on land, for alterations to suit land conditions would have involved in most cases both structural and physiological changes, some of them fundamental in nature. Possibly a few could endure brackish, or eventually even

fresh water, and remained in streams or inlets, but the majority almost certainly could not tolerate the new conditions, and followed the retreating ocean. If they did not migrate, they perished.

Smaller changes in the environment, especially those occurring on land such as a slight change of climate or of vegetation, probably presented less rigorous alternatives. As was pointed out in the preceding chapter, individual animals of today may become slightly altered structurally or physiologically so as to be capable of living in a habitat from which their unmodified relatives are barred. If these changed individuals live near the margin of their range they may migrate into some adjoining area where the other members of their species cannot follow them. Thus a new species, occupying a contiguous region, may arise. The same principle may have operated in the past, permitting migration to occur. Such modifications in animals as would fit them for slightly different environments may occasionally, where the environment itself was being altered, also have operated in a different manner and made migration unnecessary. There are some instances of ancient terrestrial animals which appear to have become modified almost simultaneously with changes in their environment. If, while a region was being slowly altered as to climate, soil, vegetation or other features, certain individual animals within the region were modified in a way which happened to fit them for the new conditions, the changed individuals could remain while the unaltered members of their species might be forced to migrate or might perish. Some biologists hold that, in case of a simultaneous change in the environment and in the animals, the change of environment caused the change in the animals. But there is much in favor of the view that the two changes were wholly independent of one another in origin. In the cases of parallel alteration of animals and environment, the two changes happened to fit each other. We are ignorant of those (perhaps much more numerous) cases in which the changes of animals and environment did not suit each other, for the animals must have perished or migrated early in the period of modification.

Migration of animals has also been helped or hindered by such changes as the formation or destruction of land bridges connecting continents. Reference to these geological changes was made in the preceding chapter to explain peculiarities of the present geographical distribution of animals. Paleontology also affords evidence of such changes. Fossil horses in Europe and America indicate a former connection between those continents. North and South America were connected up to middle Eocene time (Fig. 238, *A*) and were then separated (*B*) until late in the Miocene epoch or later when as indicated by fossils of mastodons, deer, horses, etc., migration between the two continents again became possible.

Migration of the Environment.—In the alteration of climate, topography, etc., a given kind of environment is believed to have traveled,

in some instances, across a continent during the passage of time. Case has described what he suggests to be an instance of migration of the

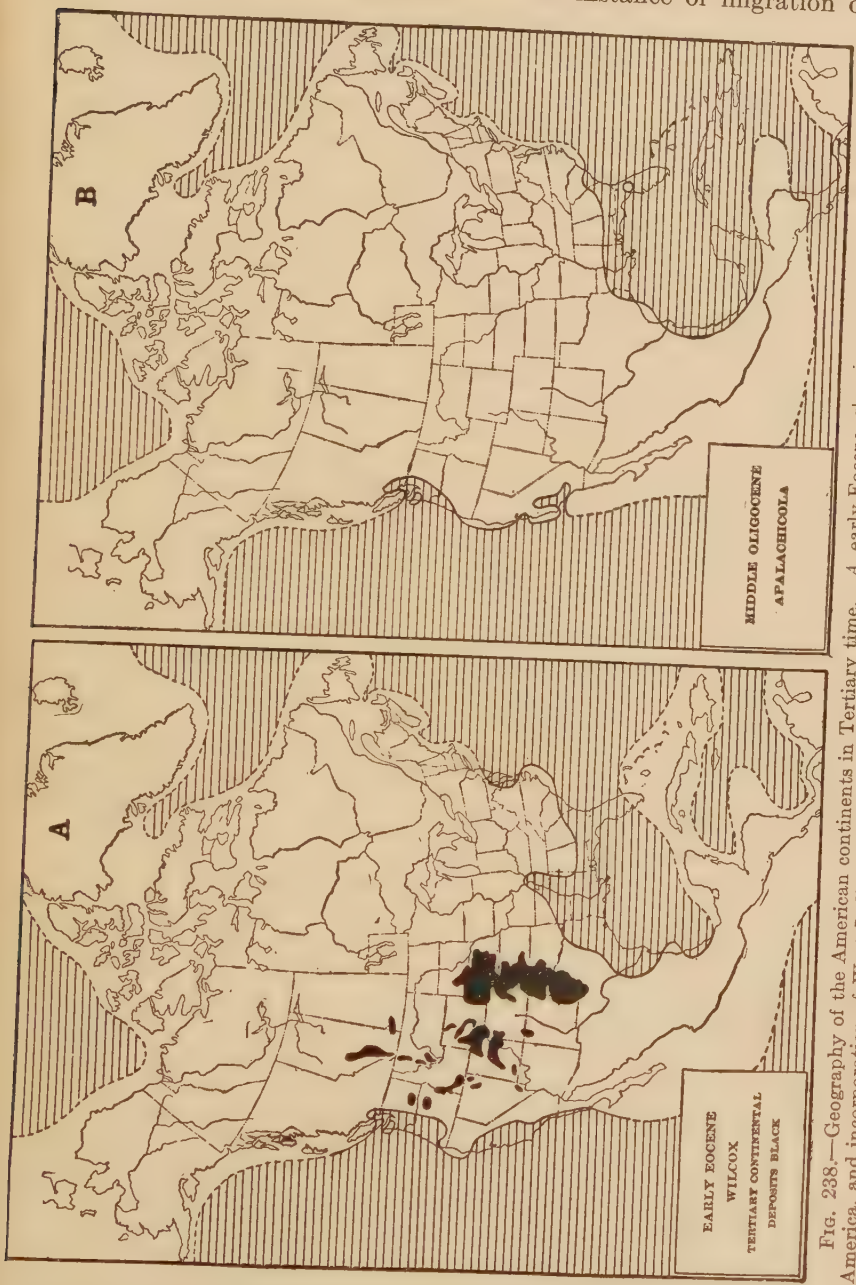

FIG. 238.—Geography of the American continents in Tertiary time. *A*, early Eocene, showing connection of North and South America, and incorporation of West Indies with the mainland; *B*, middle Oligocene, showing severance of the two continents and submergence of the islands. (*From Schuchert's Historical Geology, courtesy of John Wiley & Sons, Inc.*)

environment from Pennsylvania and West Virginia on the east to Texas, Oklahoma and New Mexico on the west. The "red beds" in the region

indicated owe their color to the oxidation of iron under certain climatic conditions existing when the deposits were formed. In Pennsylvania and West Virginia these "red beds" are found as low as the Conemaugh formation (late Paleozoic). With the rise of the land in eastern North America the climatic conditions necessary to the oxidation of iron extended farther and farther west, so that red deposits are found in the states of the southwest. But in this latter region the earliest red rocks are in the Wichita-Clear Fork beds which according to nearly all the evidence must have been deposited at a much later time than the Conemaugh beds of the east. The environment appears to have migrated across the continent during the elevation of the land, occurring successively later and later from east to west.

In harmony with this interpretation is the fact that certain reptiles and Amphibia characteristic of that age are found in much earlier deposits in the east than in the west. These animals apparently migrated westward as the environment suitable for them moved westward. This conclusion is quite in keeping with what is known of the factors of geographical distribution of animals of today. In this instance the reptilian and amphibian fossils cannot be regarded as "index fossils" by means of which the geological age of the rocks can be ascertained; they are rather "index fossils" by which certain environmental conditions can be identified.

Lines of Evolution.—The changes that occurred in the races of animals in past time, whether or not related to changes in the environment or to the migrations of the animals or their environment, were not lawless ones. Although present knowledge of the changes is often imperfect, owing to the vicissitudes to which the fossils have been subjected and to the fact that many more fossils are still undiscovered than are now in collections, there are plain indications that evolution in extinct animals was quite orderly. This statement is particularly well supported in certain cases where similar fossil animals have been found in successive geological formations representing a long period of time. When the fossils are from rocks separated from each other by comparatively short time periods, a very complete series of animal remains may sometimes be obtained. Such series have been recovered for the mastodons and elephants, horses, cephalopods, camels and others; and in each case the actual course of evolution is plainly indicated.

Evolution of Elephants.—The mastodon-elephant series shows a larger number of obvious changes than most of the other series named, all of these changes except that of the size of the body having to do with features of the head. From the numerous specimens of elephant-like forms available, the following are selected (following Lull) as probably representing a direct line of evolution: *Mœritherium* from the upper Eocene of Egypt; *Palæomastodon* from the lower Oligocene of Egypt, also

from India; *Trilophodon* from the Miocene of Europe, Africa, and North America; *Mastodon* from the Pliocene and Pleistocene of North America, Europe and Asia; *Stegodon* from the Pliocene of southern Asia; and *Elephas* from the Pleistocene of the Americas, Europe and Asia, as well as the living elephants of Asia and Africa. A study of Fig. 239 in connection with the following account will disclose the more striking steps of evolution. These forms differed from one another in a number of features, but the differences between any member of the series and the one that precedes or that which follows were so small that the series is obviously a continuous one. Mœritherium was very different from the modern elephant, but the intermediate forms completely bridge the gap. The series exhibits an enormous increase in size of body, changes in the form and size of the teeth, a reduction in the number of teeth, an alteration in the method of tooth succession, the enlargement of certain teeth to become tusks, the elongation and subsequent shortening of the lower jaw, the development of the upper lip and nose into a proboscis, and an increase in the height of the skull through the development of large cavities in the substance of the bone. These features are described in the several forms seriatim.

Mœritherium.—The earliest animal recognized as belonging to the elephant series, Mœritherium by name, was recovered from the late Eocene and early Oligocene deposits of northern Egypt. It was slightly over three feet in height. The features suggesting elephantine affinities are the high posterior portion of the skull (Fig. 239, *F'*) composed of somewhat cancellate bone, that is, bone containing open spaces; the elongation of the second pair of incisors in each jaw to form short tusks; the indication of transverse ridges on the molar teeth (Fig. 239, *F*); and the position of the nasal openings some distance back of the tip of the upper jaw, indicating probably a prehensile upper lip. There were 36 teeth, and the neck was long enough to enable the animal to put its head to the ground. It probably fed upon tender shoots and swamp vegetation.

Palæomastodon.—This form also lived in Egypt, but has recently been found in India. It dates from early Oligocene time. Palæomastodon was of somewhat larger size than the preceding form, the posterior part of the skull was distinctly higher (Fig 239, *E'*) with a greater development of cancellate bone, and the neck was somewhat shortened. The upper incisors of the second pair were more elongated as tusks and bore a band of enamel on their front surfaces. The lower second incisors were present, but not enlarged. All other incisors and the canines had disappeared. The molar teeth (*E*) resembled those of Mœritherium but were larger. The lower jaw was considerably elongated, and the number of permanent teeth was reduced to 26. The nasal openings had receded until they were just in front of the eyes, which is believed to indicate

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the existence of a short proboscis extending at least to the tips of the tusks.

Trilophodon.—Trilophodon, a great migrant and consequently widespread over several continents as stated above, exhibited in several re-

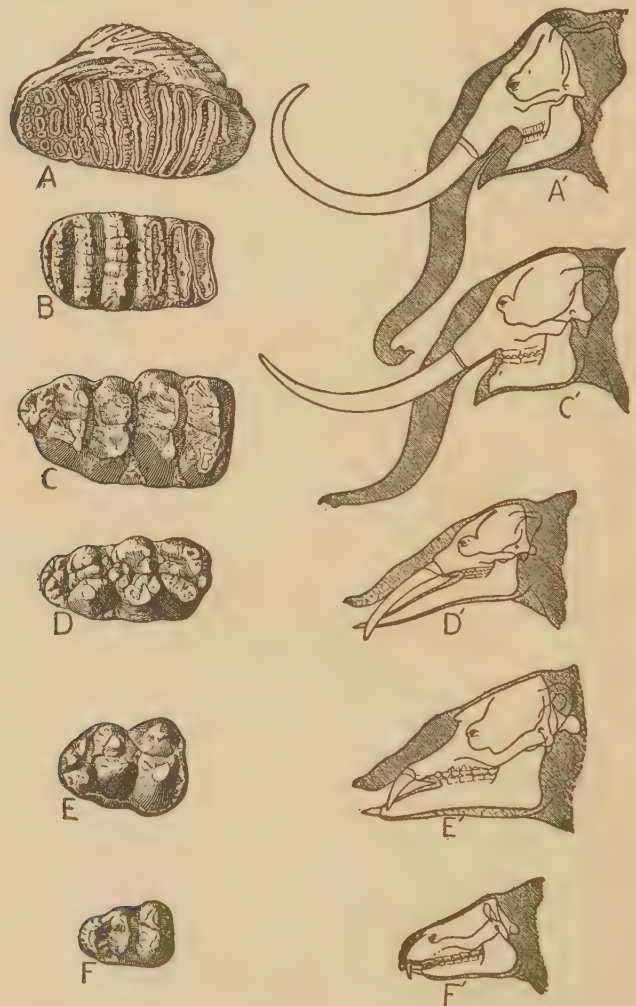


Fig. 239.—Evolution of the head and molar teeth of the mastodons and elephants. The skulls on the right are enclosed in the flesh in the form the latter is supposed to have had. *A*, *A′*, Elephas, Pleistocene; *B*, Stegodon, Pliocene; *C*, *C′*, Mastodon, Pleistocene; *D*, *D′*, Trilophodon, Miocene; *E*, *E′*, Palæomastodon, Oligocene; *F*, *F′*, Mœritherium, Eocene. (*From Lull's Organic Evolution, courtesy of The Macmillan Company.*)

spects a striking advance over Palæomastodon; but this advance was in the main in the same direction as was indicated by the change from Mœritherium to Palæomastodon. Trilophodon was a huge animal, nearly as large as modern Indian elephants. The tusks were consider-

ably longer (Fig 239, *D'*), and still bore a band of enamel. The molar teeth were large and greatly reduced in number, so that only two were present at any one time on each side of each jaw. The surface of these teeth bore a somewhat larger number of transverse crests (Fig. 239, *D*) than were present in the earlier forms. The lower jaw was enormously elongated, so that it projected as far forward as the tusks. The great weight of the lower jaw and tusks was associated with a considerable development of cancellate bone in the skull, to which the supporting muscles of the neck were attached. Presumably there was a proboscis which extended to or beyond the tips of the tusks and lower jaw.

Mastodon.—The mastodons on the whole represent a line of development which became extinct; but in their incipient stages they appear to have given rise to the succeeding forms leading to the elephants. The

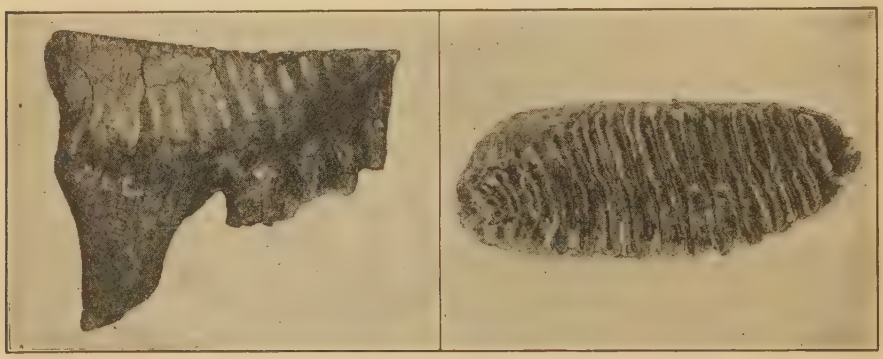
FIG. 240.—Mastodon tooth, showing the enormous cusps on the upper surface. (*From a California specimen in the Museum of Geology, University of Michigan.*)

body was somewhat larger than that of Trilophodon, being about the size of the Indian elephant. The tusks (*C'*) were much elongated (9 feet or more), but the lower jaw was greatly shortened and the lower incisor teeth were reduced or wanting. The molar teeth (Fig. 239, *C*, and Fig. 240) were scarcely more complex than earlier forms, and numbered 18 to 20 in the permanent set. They were still crushing teeth, and the food must have been tender twigs and succulent plants; indeed, remains of such objects have been found in the region of the stomach of some of the fossil mastodons.

Stegodon.—This animal is of interest chiefly because the molar teeth bore five or six well-defined transverse ridges (Fig. 239, *B*). These ridges were due to plates of *enamel* extending up through the tooth, and enclosing a substance known as *dentine*. Over the enamel in an unworn tooth was a thin coat of a third substance called *cement*, but there was not much of this substance between the ridges. In the latter respect Stegodon differed, as is pointed out below, from the elephants and mammoths

(see Fig. 241 for the tooth of a mammoth). On the whole, Stegodon was intermediate between the mastodons and elephants.

Elephas.—In this genus are included a number of extinct forms (the mammoths) from three or four continents, and the living elephants. The extinct forms, though called mammoths, were not large animals, being no larger than the Indian elephant of today, and not so large as the living African species. Some of the features of the elephants, their size, the short neck, the long proboscis, and the heavy tusks are matters of common observation. The skull is very high and short (Fig. 239, *A'*). The height is due chiefly to the development of cancellate bone, not to the enlargement of the brain which is still quite small. As stated above, the high skull affords the necessary leverage for the muscles that support



A *B*

FIG. 241.—Tooth of mammoth (Elephas) from the Pleistocene, showing the flat grinding surface and the numerous plates of enamel bound together by cement. *A*, side view; *B*, surface view. (*From specimen discovered at Ridgeway, Michigan, in* 1912, *and preserved in the Museum of Geology, University of Michigan.*)

the weight of the tusks. The molar teeth are distinctly grinding teeth (Fig. 239, *A*; see also Fig. 241). Each tooth bears a number of transverse ridges, about ten in the African elephant and two dozen or more in the Indian species. These ridges are worn down by the chewing of harsh food, so that the upper surface displays a number of flattened tubular plates of enamel enclosing dentine and bound together by cement. A tooth is completely worn out by use, and is replaced by another. The method of replacement, however, is peculiar. While the tusks (incisors) are of two sets, one following the other like *milk* and *permanent* teeth of other mammals, the grinders succeed one another in continuous fashion. There are never more than two visible grinders on each side of each jaw. As the molar teeth that appear first wear down they move forward in the jaw and are replaced by others from behind. Three permanent molars may thus successively appear on each side of each jaw, but the wearing and movement are slow, so that the interval between

the appearance of the second molar and that of the third may be 30 years. The total number of permanent teeth, including the tusks, is 14.

Correlated with the nature of the teeth of the elephants is their food and chewing habits. Whereas the ancestral forms whose molars bore prominent elevations lived on twigs and tender herbage which they *crushed* in mastication, the mammoths with their flattened tooth surfaces devoured grasses, sedges, and other harsh vegetation which they *ground* with lateral motion of the teeth upon one another. In this respect modern elephants are like the mammoths.

The changes described above constitute a classical illustration of evolutionary series. While the fossil record of the elephant is surpassed in completeness by several others, the definiteness of the changes and the size of the objects involved make it advantageous as a first example.

Evolution of the Horse.—An excellent evolutionary series is that of horse-like forms of America and the Old World. Practically the oldest recognizable equine animal is *Eohippus* of Eocene time in western North America, though Europe has a very slightly simpler animal of the same general period. Most of the development of the line of descent from Eohippus took place in North America, where, to select only some of the forms that seem to be in the direct line, there appeared *Mesohippus* in the lower Oligocene, *Merychippus* in the Miocene, *Pliohippus* of Pliocene time, and *Equus* which includes a number of Pliocene and Pleistocene fossil forms, as well as the living horses. These animals underwent changes in the feet from a three- or four-toed condition to the modern one-toed animal; the teeth, in the early forms short-crowned and capped with conical prominences on the upper surfaces, became high-crowned and wore down as they grew, so as to have flat grinding surfaces; the skull changed in proportions and in certain features of the orbit of the eye; and the body as a whole increased greatly in size.

Eohippus.—Eohippus is the first member of the series recognizable as ancestral to the horse, though it may also be regarded as appproximately representing an ancestor of the tapirs and the rhinoceroses. It stood about twelve inches high, and had a short head and neck. The hind foot had three well-developed and functional toes. On the outer side was a splint bond representing an additional toe, and on the outer side a rudiment of still another. Many living vertebrates have five digits on each hand or foot, and there is anatomical and embryological evidence that primitive vertebrates in general had five digits. These are numbered from the inside outward, the thumb or great toe being first, the little finger or little toe last. In the hind foot of Eohippus the functional toes are the second, third and fourth, while the fifth is reduced to a splint bone and the first is rudimentary. The fore foot had four functional digits, the first being wholly wanting (Fig. 242), though some old figures erroneously include one. In the ancestors of the horse the first

digits seem to have disappeared first, followed by the fifth. The teeth of Eohippus were short of crown and relatively long of root. The upper surface bore several conical cusps which, however, showed some sign of

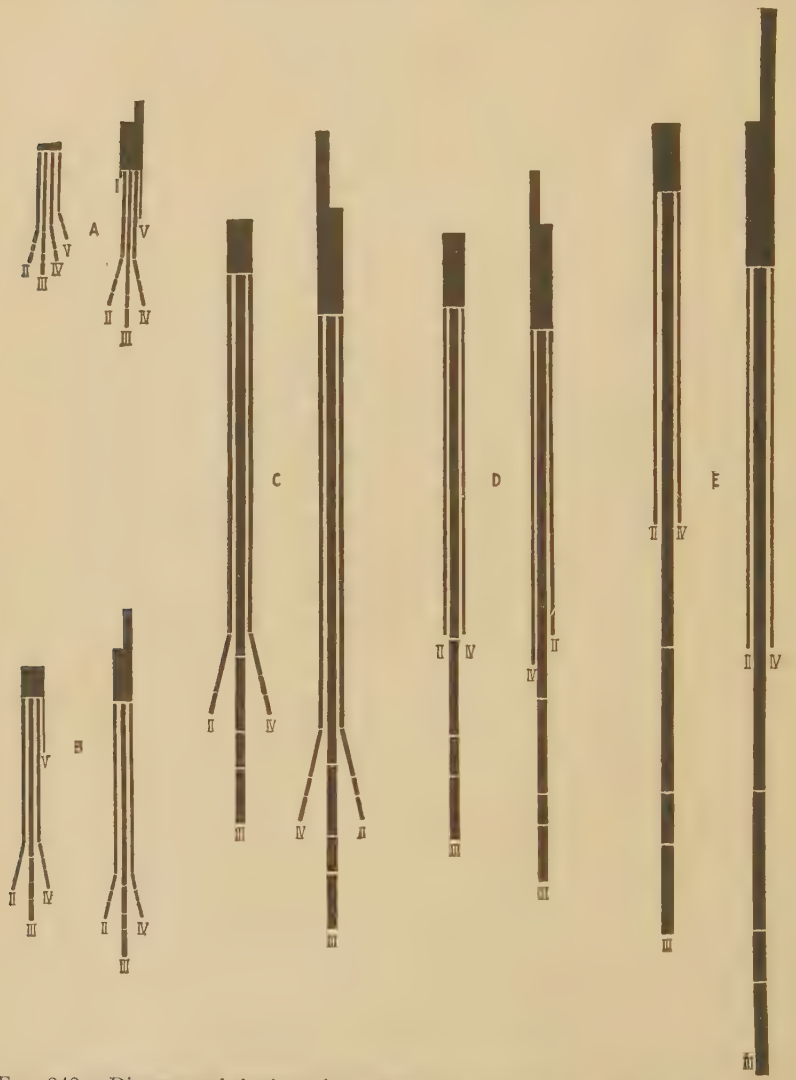


Fig. 242.—Diagrams of the feet of members of the horse series. The carpal and tarsal bones are not separately represented. The Roman numerals indicate the numbers of digits, the inner digit being designated I. *A*, fore and hind feet of Eohippus, lower Eocene; *B*, fore and hind feet of Mesohippus, lower Oligocene; *C*, fore and hind feet of Merychippus, Miocene; *D*, fore and hind feet of Pliohippus, Pliocene; *E*, fore and hind feet of Equus, Pleistocene and recent.

fusing to form transverse crests (Fig. 243). The skull (Fig. 244) was small, the lower jaw comparatively short, and the orbit was placed well over the teeth, making the face relatively short.

Mesohippus.—This animal was about 18 inches high. It had only three digits on each foot, but on the outer side on the fore foot was a

FIG. 243.—Fossil teeth of ancient horse-like animals. *a*, tooth of Eohippus with the roots broken; *b*, tooth of Mesohippus; *c*, tooth of Merychippus. (*Photographed from specimens in the Zoölogical Laboratory of the University of Michigan.*)

splint bone representing an extra toe (the fifth). Figure 242 represents the feet diagrammatically. Of the three well-developed toes, the middle

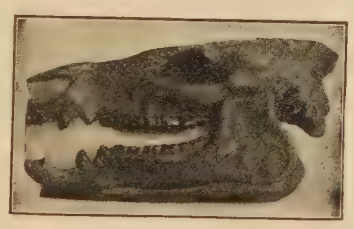


FIG. 244.—Skull of Eohippus, about $\frac{3}{10}$ natural size. (*From model prepared by Ward's Natural Science Establishment.*)

one (third) was in each foot distinctly larger than the others. The skull (Fig. 245), except for its increase in size, had not changed strikingly.

FIG. 245.—Skull of Mesohippus, about $\frac{3}{10}$ natural size. (*From photograph of specimen in Museum of Geology, University of Michigan.*)

The crowns of the molar teeth were still low (Fig. 243) and were tuberculate, that is, provided with cusps on the upper surface, but the cusps were more distinctly united into ridges or crests.

Merychippus.—The feet of Merychippus were all three-toed (Fig. 242), vestiges of the fifth toe being present in some specimens and wanting in others. The lateral toes, however, were high above the ground, thus marking a distinct advance from the condition in Mesohippus. The entire weight of the body was borne upon the middle (third) toe. Quite as important as this reduction of the lateral toes was the change in the teeth. The permanent molar teeth had moderately high crowns, and the upper surface was worn down to a flat grinding surface marked by sharp ridges of enamel set among dentine and cement (Fig. 243). Merychippus was evidently a grazing animal, whereas its predecessors must have fed upon succulent herbage which was crushed, not ground. The

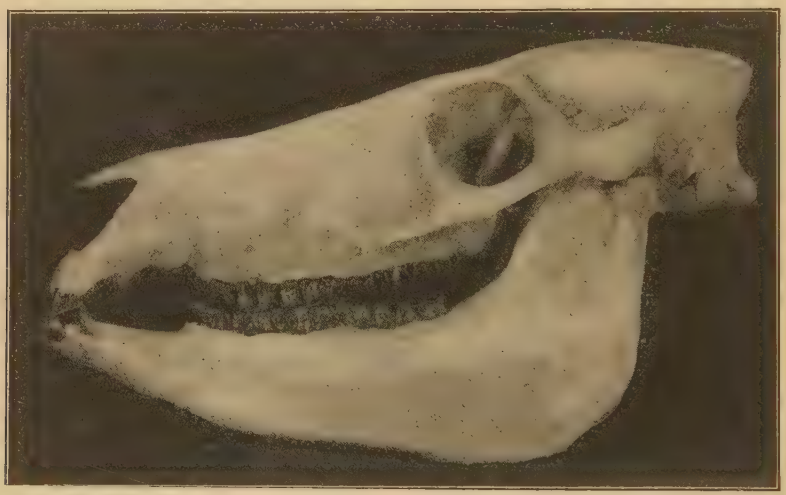


FIG. 246.—Skull of Merychippus, about $\frac{3}{10}$ natural size. (*From model prepared by Ward's Natural Science Establishment.*)

milk molars of Merychippus, unlike the permanent ones, were short-crowned and had little cement. The two sets of teeth thus showed in the lifetime of one individual changes of the same kind as were taking place in the race of horses, and recall the so-called biogenetic law (Chap. XIII) according to which the development of an individual repeats the evolutionary stages of the race to which the individual belongs. The skull was enlarged (Fig. 246), and the lower jaw was heavier in evident relation to the change of the teeth. The orbit of the eye occupied a more posterior position relative to the teeth, making the face relatively longer. The orbit was also completely closed behind by a bar of bone which in the earlier forms was merely a process projecting down from above. The body had increased to a height of three or four feet.

Pliohippus.—This animal was not appreciably larger than the preceding member of the series, but differed from it in at least one striking

feature. The two lateral toes had disappeared (Fig. 242), except as long splint bones. Pliohippus was thus the first one-toed horse. The teeth were moderately long-crowned and possessed grinding surfaces. The body stood about 48 inches high.

Equus.—The fossil horses of Pleistocene time were so nearly like the living forms as to be included with the latter in the same genus. The recent animals are 60 inches or more in height, and weigh many hundreds of pounds. Each foot has but one toe (Fig. 242), on the tip of which the animal stands like a ballet-dancer. Two lateral toes are evidenced by splint bones, and in rare cases a reversionary horse is born with externally visible digits articulated with one of these splints on each fore foot. The teeth are long and columnar, and grow continuously during early and middle life, during which time the wear at the upper surface approximately equals the growth. The grinding surface is worn flat, except that the enamel resists the abrasion more successfully than do the dentine and cement, so that the enamel forms sharp cutting ridges. The position of these ridges changes somewhat as the tooth is worn to different levels and the pattern of the upper surface is indicative, in a general way, of the age of the animal. Late in life growth of the teeth practically ceases, and then the teeth may become quite short. The skull is enlarged, particularly the front portion of it, probably in relation to the battery of large teeth which it contains. The face is relatively longer than in the ancestral forms, since the eye is set well back of the teeth and the brain case has not been relatively enlarged.

Relation to the Environment.—During Eocene time, when Eohippus lived, North America is believed to have had a moist climate with an abundance of soft or marshy ground. On such ground an animal with four-toed or three-toed feet, especially if it rested partially on the soles of these feet, could have walked more successfully than could an animal with but one toe on each foot, particularly if it stood on the tips of these toes. Later the climate became more arid, streams and lakes dried up, and the hard plains lands were developed. One-toed horses could occupy these plains successfully, and the lightening of the lower part of the legs was in the interest of speed. If, as is not improbable, the vegetation of the earlier periods was tender or succulent, while later the harsh grasses and sedges became prominent, the change in the teeth of the horse-like animals from crushing structures to grinders also served to fit the animals for the environment in which they lived. Whether the increase in size is to be regarded as an advantage is uncertain.

While the changes described above have in the main fitted the horses to live in the environment which they occupy, it is not to be assumed that the features of the environment caused the animals to change in this way. The causes of such evolutionary modifications are discussed in the following chapter.

Evolution of the Camel.—The camel family underwent most of its evolution in North America. The earliest genus recognized as ancestral to the camels was Protylopus of late Eocene time. From it appear to have sprung three lines of descent, two of which became extinct. The third led to the camels of today. Members of this third evolutionary series lived in North America until Pliocene or Pleistocene time, when they migrated to South America, Asia and Africa, and none have been recovered from later deposits in North America. In South America their descendants became the guanaco and the vicuna (both belonging to the genus Auchenia) from which the domestic llama and alpaca have been derived. In Asia and Africa the migrants gave rise to two species of camels, the one-humped Arabian camel, or dromedary, and the two-humped camel of central Asia. Both of these species are domesticated; indeed, it is doubtful whether there have been any truly wild camels in the Old World for thousands of years, since the undomesticated camels of Turkestan are probably feral, that is, they have escaped from domestication.

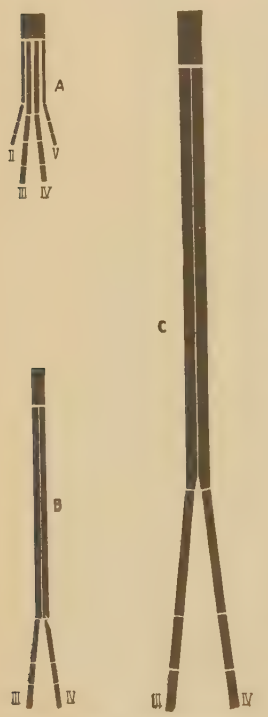


FIG. 247.—Diagram representing the evolution of the fore feet in the camel family. The carpal bones are not separately distinguished. The Roman numerals indicate the numbers of the digits, the inner digit being designated I. *A*, Protylopus, from the late Eocene; *B*, Poëbrotherium, from the early Oligocene; *C*, the guanaco, a living species.

The evolutionary changes undergone by the camels resemble to some extent those of the horse, and are described here in less detail. Protylopus, the "original" camel, was of about the size of a large rabbit. It had 44 teeth in a continuous row, of which the molars were low-crowned. The orbit of the eye was open at its posterior margin, the fore feet possessed four separate and functional toes (Fig. 247) and the hind feet two functional and two reduced toes. From such an animal have come, by changes which were not evenly distributed over the intervening ages, the guanaco, the vicuna and the huge camels of Asia and Africa. The teeth of these recent animals are but 34 in number, and are separated into several groups by wide toothless spaces. The molars have relatively long crowns. The orbit of the eye is completely closed posteriorly. The two lateral toes have been completely lost, so that no vestige of them remains, and of the two toes that do remain the metacarpals in front and the metatarsals behind have fused into a single bone in each foot, divided at the distal end to bear two distinct series of phalanges. The structure of the toes is such as to allow them

to spread, and a pad has been developed beneath them. Nothing is known of the evolution of the hump, since this elevation is merely a mass of fat varying in size with the state of nutrition of the animal, and is not correlated with any peculiarity of the skeleton.

Evolution of the Cephalopods.—An excellent fossil record among the invertebrates has been established for the tetrabranchiate (four-gilled) Cephalopoda (Mollusca). This branch of the cephalopods is represented today by Nautilus, which lives in a coiled shell, externally resembling a snail shell. The animal lives in only a small portion of the shell near the aperture, however. The rest of the shell is divided by partitions into a

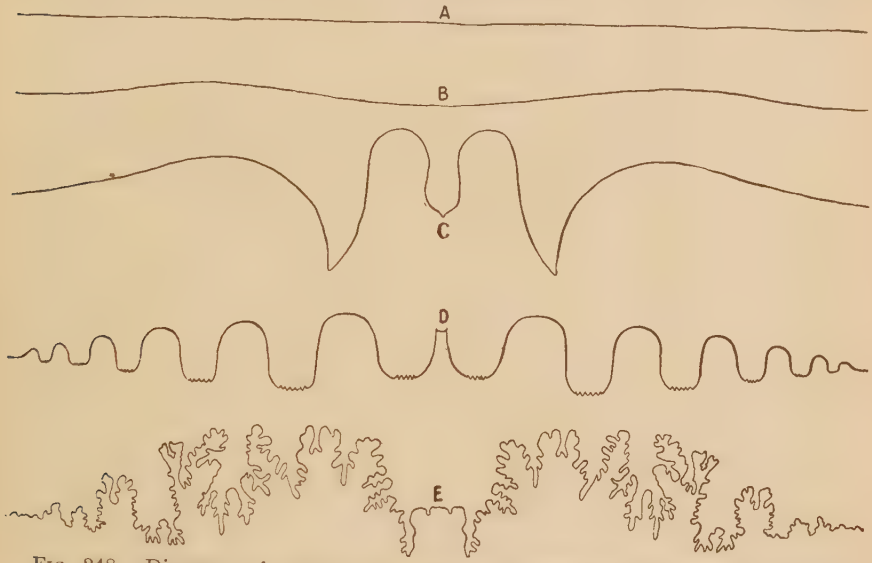


FIG. 248.—Diagrams of sutures of cephalopods, represented as spread out with the ventral point in the middle. *A*, orthocone; *B*, nautiloid; *C*, goniatite; *D*, ceratite; *E*, ammonite.

number of chambers, from which the animal is excluded. These partitions, or septa, represent the positions occupied by the animal earlier in its life. As the body grows, it moves periodically forward into the wider part of the shell and secretes a partition behind itself each time it moves.

Tetrabranchiate cephalopods have been found, as fossils, in Cambrian rocks. They became fairly abundant in the early Ordovician time. At that time, unlike the modern Nautilus, their shells were straight cones (*orthocones*). All later forms appear to have descended from these orthocones. Fossil cephalopods are found in the strata of all periods from the Ordovician to the Cretaceous, and as stated above a few members of the group are still living.

The course of evolution was as follows. The shell soon began to bend, and in many forms became closely coiled in flat spiral form like

the shell of some snails. Owing to their resemblance to Nautilus these animals are called *nautiloids*. They were very abundant in Silurian time. Up to this period the septa across the shell were flat and saucer-like, and the *sutures*, the lines of junction of the septa with the wall of the shell, were nearly straight or only slightly curved. Later the septa became bent in various ways, at least at their edges, so that the sutures were curved or angular (see Fig. 248). Forms whose sutures were of this curved and angular form are called *goniatites*, and they were abundant in the Carboniferous period. These were to a large extent superseded in Triassic time by other genera, still tightly coiled but with sutures thrown into a number of regular curves and sawteeth, which may be described as "crooked." These forms with crooked sutures are known as *ceratites*, from a very common genus Ceratites. And finally, in the forms known as *ammonites*, the sutures became finely crimped in a compound fashion, often producing most exquisite foliaceous patterns. Fossil ammonites are most abundant in the Jurassic to Cretaceous strata.

Though there were many irregularities and overlappings in the series of tetrabranchiate cephalopods, the fossils show on the whole clear evidence of progress from a straight shell to one tightly coiled, and from nearly straight sutures to sutures that were bent, angular, crooked, and finely lobed.

Relationships of Living Animals.—The existence of fossil records demonstrating step by step the origin of animals now living from more primitive ancestors can hardly escape throwing light upon obscure relationships of modern groups. Even when series as complete as the ones described above are lacking, fossil animals intermediate between two living groups may create the presumption that both groups have sprung from a common stem. Thus the reptiles may be traced to an amphibian ancestry through the Stegocephali, the armored Amphibia of the past. Birds are assigned a reptilian origin through Archæopteryx (Jurassic), a reptile-like animal which had feathers. Mammals have been derived from reptiles, as indicated not only by fossils but also by the facts of structure and embryonic development. The paleontologist is called upon to make decisions regarding the relationships of taxonomic groups of both high and low rank. He is most successful in establishing the connections between classes, orders and families; but attempts to solve problems of generic and specific rank are made with as little hesitation as in the case of living animals.

Extinction of Groups.—Everywhere in the rise of the animal groups of today there have been tragedies more thrilling than the memorable catastrophes of historical times among men. Races have come into being, have passed through a series of changes, and then perished. Sometimes what may be regarded as the main line of development was pre-

served, while only the offshoots were lost. At least, in those cases, the modern animals represent as complex an attainment as the lateral lines which disappeared. In other cases, the climax of the series was extinguished, while all that now remains is from the primitive early members of the stock. In the horse series, we have left today the most highly modified member, while its less specialized ancestors and several less specialized lateral branches have been lost. In the elephants and camels, also, the greatest amount of modification of which we gain any knowledge from fossils is preserved in the modern animals, while only the forebears and several sister lines of less complexity have met extinction. In the cephalopods, however, the maximum development was lost. The forms with bent, crooked, and foliaceous sutures are known only as fossils, while the living forms of today are almost identical with the nautiloids, whose sutures were only gently curved. If, as is naturally assumed, the Nautilus of today is the practically unaltered direct descendant of the nautiloids of Silurian time, relatively primitive forms have been preserved while the highly specialized have perished.

Among the reptiles, too, great specialization led to extinction. The reptiles rose to a dominant position in the Mesozoic era, which is known as the Age of Reptiles. They spread over most of the earth, and North America was an important scene of their development. Some were small animals, others as large as the largest whales. Their skeletons show the largest ones to be of 60 to 80 feet in length; such animals in the flesh must have weighed many tons. But they did not specialize in size alone; they exhibited a variety of structure. Some were lizard-like and evidently ran low upon the ground, while others stood high on their legs. Some bore their weight on all fours; others, as indicated by two-footed tracks and the size of the bones, ran upon their hind legs. The forelimbs of the latter were used only for grasping. Necks and tails were long and slender in some, short and stout in others. Many of them were armored in striking fashions. Curious armatures had arisen before Mesozoic time, for Edaphosaurus (Figs. 249 and 250), a Paleozoic form, had long spines on its back joined together like a fin. It was in the dinosaurs of the Mesozoic era, however, that bizarre external structures attained their greatest diversity, as exemplified in the rows of flat plates of Stegosaurus (Fig. 251), and the curious horns on the head of Triceratops (Fig. 252).

The group of dinosaurs, dominant among the reptiles, of multitudinous form and high specialization, took its rise in the Triassic period; underwent its evolution in early and middle Mesozoic time; reached the extreme specialization described above in the Cretaceous period; and then perished. The reptiles of today are all much less specialized. The nearest modern reptilian relatives of the dinosaurs appear to be the crocodiles, of which there are but few species and none of them are highly

specialized. In this case, as in the cephalopods, the most highly specialized branches of the group became extinct, while the more primitive survived.

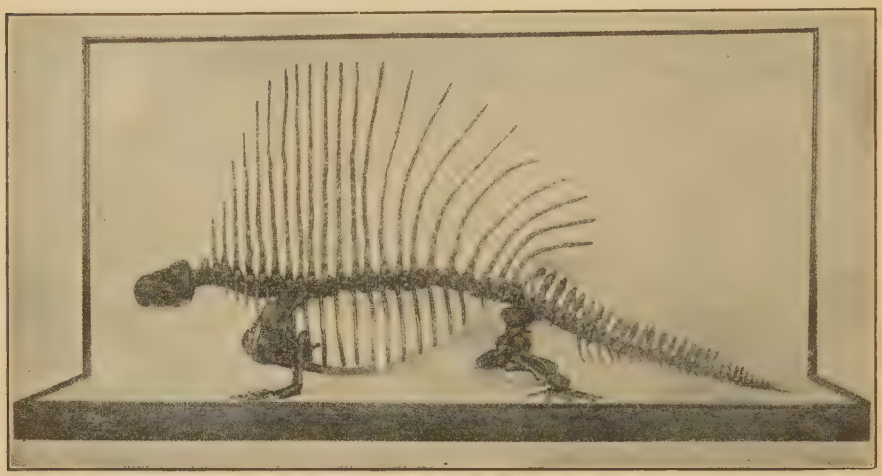


FIG. 249.—Skeleton of a Permo-Carboniferous reptile, *Edaphosaurus cruciger*. (*From a specimen in the Museum of Geology, University of Michigan, mounted under the direction of Prof. E. C. Case.*)

The cause of the extinction of whole groups of animals is unknown. One can but conjecture the factors responsible for the demise of the offshoots of the family tree of the horse; for the loss of the collateral lines

FIG. 250.—Restoration of the reptile *Edaphosaurus cruciger*. (*By Prof. E. C. Case.*)

among the elephant's kindred; for the failure of the ammonites in the cephalopods' struggle for existence; and for the extinction of the reptilian aristocracy, the dinosaurs. Many surmises have been offered.

Most suggestions are to the effect that these animals found themselves in an unsuitable environment and that the environment became inhospitable through geological or climatic changes or through the rise of other

FIG. 251.—Skeleton of the armored dinosaur Stegosaurus. (*From Lull's Organic Evolution, courtesy of The Macmillan Company.*)

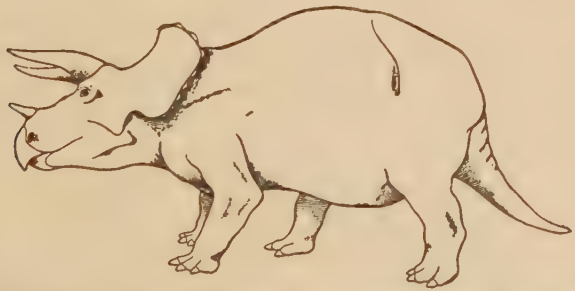


FIG. 252.—Restoration of horned dinosaur Triceratops. (*After Lull, from Schuchert's Historical Geology, John Wiley & Sons, Inc.*)

(inimical) forms of life. The fantastic forms and the huge size which the dinosaurs, for example, assumed can hardly have been responses to factors in the environment. The evolution of these reptiles was prob-

ably started and directed by forces within the animals, independently of external conditions. What these internal forces may have been can only be conjectured, but some possibilities are pointed out in the following chapter. Changes in the environment, therefore, can hardly be supposed to have modified this evolution, nor to have arrested it except by destroying the race. If considerable changes in the environment took place in late Cretaceous time—and such changes must have occurred repeatedly—they could easily have resulted in the extinction of the dinosaurs. It is not proven, however, that this has been the method by which evolutionary cycles terminated.

It may be pointed out that nations of men have also risen to prominence in the world, have been leaders for a period, and then sunk into oblivion, to be succeeded by other nations. However, the origin and extinction of animal races and the rise and fall of nations may have nothing in common, except the fact that no one knows the cause of either phenomenon.

Prehistoric Man.—The difficulty in an attempt to relate the rise and fall of nations of men to the evolutionary cycles of other animals is that nations are usually not biological units. They are political units, often held together by common language or by force, and with few exceptions do not represent racial unity. Abandoning, however, the artificial classification of men into peoples, and regarding the human race as a unit, we may find in man the same progressive development as in any of the other great groups of animals which once held a dominant place in the world. Man has had his rise, as did the reptiles, and before them the Amphibia and fishes. Whether he is also to experience a decline and extinction remains for the future to reveal.

Structurally man plainly belongs to the Primates, an order of mammals including the monkeys, marmosets, baboons, gorillas, and the like. To some of these animals he bears much more resemblance than to others. Thus, there is no question that the anthropoid apes stand much nearer to man, structurally, than do the other primates. Were one to look for evidences of genetic relationship of man to the other mammals, structure would point to these apes as furnishing the nearest living connection.

Actual establishment of this connection through fossil remains has been long delayed. Even now it rests on a series of fragmentary remains which, when compared with the reptilian, cephalopod, or mammoth record, appears meager. Taken in connection with the anatomical evidence, however, there is scarcely room to question the common ancestry of man and the apes.

The Java "Man."—The oldest fossils showing more than ape-like resemblances to human beings were found by a Dutch military physician on the island of Java in 1891 and 1892. They consist of a skullcap, a left femur, and several teeth (molar and premolar). Though these

fragments were found at distances of some feet from one another and at different times, they could not belong to any of the numerous other fossil animals found in the same excavation, and are believed to belong to the same individual. The femur is nearly straight, indicating that the animal stood and walked erect, and its length is that appropriate to a body about five and one-half feet tall. This feature is therefore distinctly man-like. The teeth are more robust than human teeth, and their roots are strong and quite divergent as in the apes; but the crown is wider from side to side than from front to back, probably indicating that they were crowded into a shorter linear space, which is more like human teeth. The skull cap indicates a brain cavity of about 850 cc., whereas that of the larger apes is about 600 cc. and that of savage man is about 1,000 cc. A conjecture as to the appearance of this being in the flesh is portrayed in Fig 253 (left). Such restorations are of course quite speculative.

The name *Pithecanthropus erectus* has been given to the animal to which these remains belong. The other fossils found with it indicate that it belongs to upper Pliocene or lower Pleistocene time, or perhaps half a million years ago. It is not now thought that Pithecanthropus stands in the direct line of human descent. Nor is it certain that it has any relation to the evolution of man. Certainly this animal possessed several characteristics more nearly like those of man than are those of any of the living anthropoid apes, and several that are more ape-like than any present-day men. What further study of the specimens may reveal can only be conjectured.

Various archæologists and paleontologists have held that man existed at a time even earlier than Pithecanthropus, that is, in distinctly Pliocene or even Miocene time. Their argument is based partly on evidences of culture, partly on fossils supposed to be of an earlier age. Bones perforated or marked with incisions are thought by some to be the work of men, certain flints are supposed to have been shaped by fire or by mechanical means in the hands of intelligent beings, and crevices containing animal remains have been regarded as pitfalls or traps set by human hunters. These objects date from Pliocene or earlier time. Some of them, the flints, for example, are found, however, in deposits as early as the Oligocene or even Eocene. Objects as ancient as these can hardly have been formed by man. The fossils also are not satisfactory as evidence of human beings earlier than *Pithecanthropus erectus*. Boule, in a critical review, rejects the altered bones and flints and traps in the belief that these are due to natural agencies, and the fossils on the ground that they are much more recent than some have supposed, and concludes that there is no satisfactory evidence of man earlier than the end of the Pliocene period.

The Heidelberg Man.—The next most remote fossil resembling man was discovered at Mauer, near Heidelberg, Germany, in 1907, about

eighty feet below the surface. Only the lower jaw was recovered. It is very massive, the ascending posterior branches are extraordinarily wide, and there is no chin. In all these respects it is much more like the jaw of apes than like that of man. The teeth, however, are nearly like those of living savage races of man. The row of teeth is a parabola, not a capital U as in the apes, the canines do not project above the level of the other teeth, and the molars are about as wide as long (in apes longer than wide). The teeth are actually large, but are relatively small for the heavy jaw in which they are set. The characters of the teeth that are ape-like are those in which the apes resemble savage human races. For example, the posterior molars have five cusps, as do apes and savage men, while civilized men have but four. In like manner, the pulp cavity of the Heidelberg teeth is large as in savage human races and apes, but unlike civilized men.

The fossil animals found in the same strata with the Heidelberg jaw include a variety of vertebrate forms mostly related to early Pleistocene time. One estimate in years puts the period of the Heidelberg man about 300,000 years ago.

The Piltdown Man.—Fragments of skull bones attributed to primitive man were found in a flint bed being worked for road material, at Piltdown, in Sussex, England, in 1911 and 1912. What was apparently a nearly complete skull was badly broken by a workman's tool, and only a few fragments large enough to be of value were recovered. Among the pieces was the right half of the lower jaw. Several years later additional fragments of one or two other individuals were obtained near the same place. The fragments of the skull do not permit of accurate restoration, but the brain cavity was evidently much larger than that of apes. Although the skull bones are nearly twice as thick as those of modern men, the Piltdown skull could be regarded as human. The jaw, however, is very ape-like. Thus, the canines are large and higher than the other teeth, and certain minor features are distinctly simian, so that the jaw as a whole and in detail is much like that of a chimpanzee. Paleontologists were at first in doubt, and some still are, whether the skull and jaw belong to the same individual. Recent study indicates that the skull is perhaps somewhat less human than was at first supposed, and this fact and the later discovery of parts of different individuals at the same place lead to the view that the several fragments do belong together.

The stratigraphic evidence indicates that the deposits containing the Piltdown fossils are of early Pleistocene age, and nothing in the other fossil animals nor in the signs of culture disproves that conclusion.

The Neanderthal Man.—The name of this near-human type comes from the discovery of a skullcap and several long bones in a ravine called the Neanderthal, near Düsseldorf, Germany, in the year 1856. A skull

of a similar type had been found as early as 1848 at Gibraltar, but it was not described until later. A jaw of like characters was found near Dinant, Belgium, in 1866, and a skull at Spy, Belgium, in 1886. To these have been added many other specimens, discovered in the period from 1899 to 1912, coming from Croatia and France, and representing almost every part of the skeleton. These parts, in so far as they duplicate one another, are closely similar and all are referred to the primitive type known as the Neanderthal man. The frontal region of the skull is receding, the ridges over the eyes are heavy, the posterior portion is projecting and depressed, the face is long and protruding, the orbits are large, the jaw robust, and the chin rudimentary. In most of these

FIG. 253.—Restorations of prehistoric men. Left, *Pithecanthropus erectus;* middle, *Homo neanderthalensis*, modeled on the Chapelle-aux-Saints skull; right Crô-Magnon man modeled on type skull of the race. *(From original busts by Prof. J. H. McGregor.)*

respects the Neanderthal skull is intermediate between the larger apes and civilized man. The brain cavity varies considerably, in one specimen being fully as large as highly civilized races of today, in other specimens somewhat less than that of modern men. The teeth are distinctly like those of uncivilized modern men. Other parts of the skeleton (vertebræ, ribs, arm and leg bones) show various degrees of approach to the modern human type. The stature of the Neanderthal man was somewhat less than the average of modern human races.

One of the best-known specimens is shown by accompanying fossil animals and by stratigraphy to belong to middle Pleistocene time, while the flints found with it are of a cultural age corresponding approximately with the late Pleistocene. In years, according to one estimate, the period of the Neanderthal type was not less than 100,000 years ago.

The Race of Crô-Magnon.—Numerous skeletons and parts of skeletons having many features in common have been referred to this so-called race. All are distinctly human, showing few characters that are more ape-like than modern man. The skeletons are quite variable, however, and probably should be grouped in three different varieties. All have been found in western Europe in contemporaneous or nearly contemporaneous deposits, but probably arose from three sources.

One of these three types, the Crô-Magnon race proper, is so named from the discovery near Crô-Magnon in France, in 1868, of five skeletons along with bones of other animals, molluscan shells and flint instruments. Others have since been taken in England, Belgium, and elsewhere in France. The body was tall (about six feet), the skull was somewhat larger than the average skull of modern men, and the frontal region high. The last feature is believed to indicate high intelligence, which is confirmed by carvings and works of sculpture. The restoration in Fig. 253 is accurate so far as measurements are concerned, but the facial expression is conjectural. This race appears to have originated in the Mediterranean region and to have developed in central and western Europe.

The other two varieties mentioned above, while occurring with Crô-Magnon man and often regarded as of the same race, differed from the type described in certain respects. One of them was distinctly shorter, possessed certain negroid characters including a broad nose, and probably migrated from Africa. The other was also shorter, its face was high and wide, but flat, and it was much like the modern Eskimo. It probably came to western Europe from the north in late Pleistocene time and retreated to the north in a later period.

Relation of Fossil Man to Living Man.—Although the man-like beings described in the several foregoing paragraphs are in various ways intermediate between the higher apes and man, there is no proof that any of them stand in the direct line of human descent. The weight of present opinion is that they are not direct ancestors of modern man, but that they belong to collateral lines. At least it is practically certain that the bulk of the civilized races of today have come from places where the fossil forms are not known ever to have been. This does not necessarily mean that none of the fossil types has left any descendants. Some paleontologists have suggested that the Eskimos of today have sprung from one of the types associated with Crô-Magnon man, though this is probably incorrect. Others have pointed out that men almost identical with the true Crô-Magnon type are still living in the Canary Islands and in the Dordogne in France. Where one must look for the ancestors of the white races of America and Europe is uncertain. The majority of paleontologists and anthropologists have regarded Asia as the place of origin. Some explorations have recently been made in that

continent, others will doubtless follow, and one may fairly hope that further light will soon be shed on the question.

The Nature of Paleontological Evidence.—Fossils, as even the brief account in this chapter will show, constitute some of the very best evidence regarding the fact of evolution. In this respect, paleontology differs from most other sources of information concerning evolution in the distant past. When the study of comparative anatomy reveals likenesses in different animals, one can only infer that these likenesses are due to inheritance from a common ancestry. When comparative embryology shows similarities in the embryos of two groups of animals, one can only assume that the course of development is brought down from a common forebear. And when the present distribution of animals seems to require that two groups should have sprung from a single antecedent group, it is nevertheless only an assumption that they did thus diverge. The conclusions stated above are plausible, but they are necessarily only inferences. It is otherwise with the facts of paleontology. They leave no doubt that animals were different in different periods; for there are the remains to prove it. There is usually no need to argue which are the earliest forms, for the age of the rocks in which they lie can in general be ascertained in other ways. Often, unless there are long gaps not bridged over, the course of evolution is clearly mapped out; for in successive layers of rock are the remains that show by just what steps a given kind of animal evolved.

Paleontology occupies this favored position as evidence of evolution only so long, however, as it is concerned merely with the fact of evolution and with the course which evolution has taken. As soon as the facts of fossils are used to make incursions into other fields, inference is necessary. From a flat-crowned tooth one may infer that the owner was a grazing animal, but that is not proven. Restorations of extinct animals in the flesh are inferences based on a knowledge of modern animals. From a facial angle a certain degree of intelligence may be inferred, but only inferred. The ridges on a bone may indicate heavy muscles, but they lack something of proof. In particular, fossils offer no evidence regarding the cause of evolution. It may be easy to devise plausible explanations for the changes that animals have undergone; but for proof of the correctness or incorrectness of these explanations facts have to be gathered from other sources.

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CHAPTER XVII

EVOLUTION

From specific statements made here and there in the foregoing chapters, and from inferences inevitably drawn from various facts therein related, the student can hardly have escaped drawing the conclusion that the animals of today are not like the animals that once inhabited the earth. Such a conclusion will have been strengthened by much that is discovered at first hand in the laboratory. To explain many of the facts of structure and development in living organisms, the nature of fossils, and the distribution of living animals and plants, it seems necessary to assume that species have undergone gradual changes. This gradual change is called *evolution*, and species are said to have *evolved*. Man has been one of the products of evolution no less than other animals. Not one species of living organism has escaped the modifications that constitute evolution. Though some kinds of organisms have been relatively constant, while others have been altered rapidly and often, there is no species alive now which is not different from its most remote ancestors. Close similarity between modern and ancient life is limited to low forms. Nor has evolution been confined to the past; it is going on today. Not every species is evolving now, so far as can be discovered, but some species are. A few years or a few centuries hence, the species now undergoing modification may have reached a fairly stable condition, and other species, now apparently constant, be in a period of alteration.

Darwin and the Rise of the Evolution Theory.—A brief historical account of ideas of evolution has been given in the first chapter. As was pointed out there crude ideas of evolution were held by individuals even among the early Greeks. Noteworthy theories were proposed by Lamarck and others at the end of the eighteenth century and in the early nineteenth century. Wide acceptance of the doctrine of evolution, however, dates only from the time of Charles Darwin (Fig. 254) who has the distinction of having brought together so many facts indicating evolution, together with a theory to account for the facts which was so plausible, that thinking people were everywhere driven to adopt his views. The life of Darwin and the history of the evolution idea as developed by him stand, therefore, in much the same relation to the evolutionist as do the great epic poems to the student of literature or the story of the Magna Charta to the historian of constitutional government. A brief account of the origin of modern ideas of evolution may well be added to the general statement made in Chap. I.

Darwin was tremendously influenced by the work of the famous geologist, Sir Charles Lyell (Fig. 255). Lyell attempted to explain past geological changes by processes going on at the present time. If geological changes in the past of which we have present-day evidence in the form of rock strata, configuration of land surfaces, continental forms, submerged islands, and the like, could be explained by such processes as erosion, rising or sinking of the land or sea floor, and volcanic action, which are now going on, Lyell insisted that such explanations should be employed. No processes of a different order from those of the present time should be appealed to unless present-day occurrences do not explain. This insistence on the application of modern processes to the explanation of past events is known as the doctrine of *uniformitarianism.*

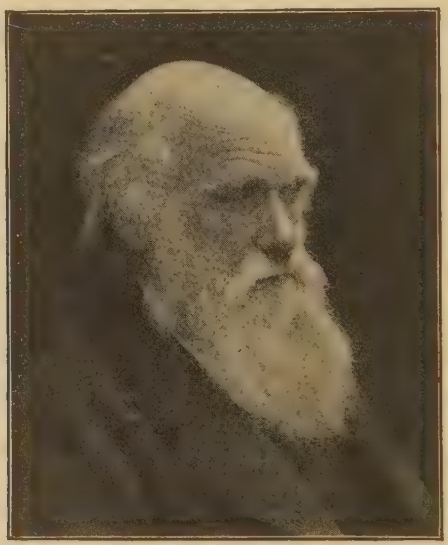

FIG. 254.—Charles Darwin, 1809–1882. (*From University Magazine. Photograph by Leonard Darwin.*)

Darwin believed that this doctrine could be applied to living organisms as well as to rocks and hills and shore lines. He had made a voyage around the world, in 1831 to 1836, as naturalist of a surveying party on the ship *Beagle.* Most of this voyage was devoted to the shores of South America. Darwin had opportunity to make long excursions on land, and observed many remarkable phenomena from which be began to suspect the mutability of species. After he returned from the voyage on the *Beagle,* he thought it worth while to open a notebook (in 1837) in which he jotted down everything that came to his notice that seemed to bear on the question of the fixity or changeability of species. For twenty years he collected such information as industriously as his health would permit. He had a happy faculty of using others to help him in this

work. He was constantly in correspondence with animal breeders, many of his conclusions were drawn from studies of animals and plants under domestication, and he was the first to be willing to use knowledge so gained to argue concerning living things in nature. Often he asked others to make observations or perform experiments for him. As a result he had a mass of evidence which seemed to him to point strongly to the conclusion that animals and plants are now in the process of evolution, that they have evolved in the past, and that the things which are causing evolution now caused it then.

His first idea as to the cause of this evolution was gained in 1838 from the reading of a book by Malthus, "Essay on Population," in which it was pointed out that overpopulation led to a struggle for existence.

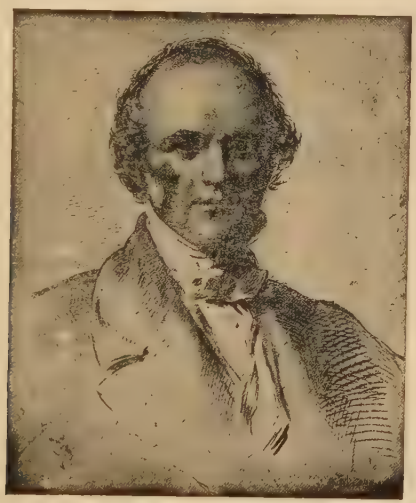

FIG. 255.—Sir Charles Lyell, 1797–1875. (*From Schuchert's Historical Geology, John Wiley and Sons.*)

Darwin was at once struck with the idea that

Under these circumstances favorable variations would tend to be preserved and unfavorable ones to be destroyed. The result of this would be the formation of a new species. Here then I had at last got a theory by which to work, but I was so anxious to avoid prejudice that I determined not for some time to write even the briefest sketch of it. In June, 1842, I first allowed myself the satisfaction of writing a very brief abstract of my theory in pencil, in thirty-five pages, and this was enlarged during the summer of 1844 into one of 230 pages.[1]

During the twenty years and more in which Darwin was collecting data he had opportunity to test this theory, which has since been called the theory of natural selection.

[1] DARWIN'S Autobiography, in his "Life and Letters."

All this time Darwin had published nothing of his discoveries. He wanted to be very sure of his ground. He had confided his ideas to only a few friends, among them the botanist Joseph Hooker and the geologist Sir Charles Lyell. It is doubtful whether he would have published as early as he did but for a curious coincidence. In 1858, Alfred Russel Wallace, an able young naturalist then in the orient, sent to Darwin a sketch of a theory of which he desired Darwin's opinion. To the latter's surprise, this theory proved to be no other than the theory of natural selection, of survival of the fittest; and as Wallace afterwards related he had first got the idea from reading the work of Malthus, "Essay on Population." At first Darwin was inclined to withhold his own manuscript, and allow that of Wallace to be published. But since Wallace's idea was admittedly a sudden one, in favor of which he had collected no facts whatever, whereas Darwin had long been gathering data relative to it, Darwin's friends protested. It was finally arranged to present extracts from both Darwin's and Wallace's manuscripts simultaneously to the Linnæan Society of London, which was done in 1858. History has adjudged practically the entire credit for the theory of natural selection to Darwin; but it is to the immortal honor of both of its authors that neither allowed a dispute regarding priority to mar the launching of their epoch-making hypothesis.

Darwin's theory was developed at length in "The Origin of Species," published in 1859. At intervals after that date he published books on specific phases of the evolution problem. New hypotheses were from time to time advanced, which were intended to supplement the theory of natural selection, such as sexual selection, pangenesis, and others. Of Darwin's writings subsequent to 1859, his "Animals and Plants under Domestication" is at once the most readable and most important. Practically all of these books are so written as to be intelligible to persons without biological training. To this circumstance, more than to any other, perhaps, is due the rapid acceptance of the evolution doctrine. It is true, the time was ripe for such an advance; and then there was Huxley (Fig. 256), who championed Darwin's views in popular lectures. But it is doubtful whether evolution would have occupied the attention of the laity, had it not been for the non-technical presentation of it which Darwin himself gave in his books.

Evolution was not accepted without opposition. The churchmen were reluctant to regard the story of the creation in any other than a strictly literal way. In the main, however, they watched the progress of the new doctrine with good nature, and at present the leading clergy of most churches are as firmly convinced of evolution as are the biologists. Occasionally even now there is a cry that evolution is being abandoned by scientific men, but the arguments in support of such a statement are usually found to confuse the *fact* of evolution with the *cause* or *method* of

evolution. When some leading biologist attacks the theory of natural selection, as has been done time and again, some one may proclaim that the doctrine of evolution has been relegated to history. Nothing is farther from the truth. It is only the theories that would account for evolution, or theories that concern the course which evolution has taken, that are still the subject of controversy.

The history of the evolution idea in the last forty or fifty years has been the accumulation of new facts in support of it, the development of theories to account for it, the grouping of animals on the basis of the relationship implied in evolution, and the application of corollaries of evolution to other branches of biology. Since a discussion of these later

FIG. 256.—Thomas Henry Huxley, 1825–1895.

developments often involves the subject matter of the other branches, any further references to the history of the doctrine of evolution that seem desirable will be made in connection with the evidence of evolution and the theories of its causes in the following pages.

Evidence of Evolution.—Before proceeding to the implications of evolution, it will be profitable to review the evidence on which belief in the changeability of species is based. The best evidence of any process is to witness it going on. If species can be shown to change while under observation, the best possible evidence of evolution has been obtained. Whenever one or more members of a species possess a characteristic not found in other members of the species in the same generation, or in preceding generations, evolution has occurred, provided the new feature is of such a nature as to be inherited. The heritability of the new feature is insisted upon, as otherwise the change would be temporary. There are

numerous differences among organisms belonging to the same line of descent; but in large part these differences are due to the environment and in the main are probably not inherited. Such non-heritable differences are known as *fluctuating variations* and have no influence upon evolution. Occasionally, however, new characters appear which are inherited. These are called *mutations,* early knowledge of which was largely due to Hugo de Vries, and every mutation is a step in evolution.

Witnessing evolution thus consists in discovering mutations as they occur. This has been done in a considerable number of instances. One of the most fruitful sources of mutations has been the small fruit fly Drosophila extensively studied by T. H. Morgan and others. Owing to the ease with which this fly is reared in confinement, upon the cells of yeast, it has been used much for experiments. At first its value as a means of studying evolution was not fully appreciated. It was bred in the laboratories of several universities for the purpose of testing the effectiveness of selection and the influence of the environment, and for experiments upon fertility, length of life, and the like. Then mutations began to appear. It is possible that mutations had been appearing at intervals previously, but if so they did not attract attention. At any rate, mutations so striking that they could not be overlooked occurred. One was a change from the normal red eye of the wild fly to a white eye. Since the flies were examined with a microscope, it is not likely that any such striking alterations escaped observation. The one fly with white eyes was probably the first that had been produced since the stock of flies in which it appeared had been taken into the laboratory. Moreover, when this white-eyed fly was bred with others, the absence of red pigment in the eye was definitely inherited as a recessive trait. Mendelian rules were clearly followed, and the case of white eye in flies has been used in the chapter on Genetics, as an example of sex-linked inheritance typical of various animals. White eye in Drosophila, then, is a new characteristic which is inherited. It is therefore a mutation and a step in evolution. There are now many white eyed fruitflies—in captivity. Perhaps, had the first white-eyed fly occurred in nature, it would have perished. Nevertheless, its occurrence would have been a case of evolution. The effect of the death of individuals in which mutations have occurred is discussed later.

Other changes have occurred in the same species of Drosophila (see Fig. 257). Eye colors other than white, to a few of which the names eosin, vermilion, cherry, buff, and tinged have been given, have appeared. New shapes and sizes of wings have occurred. In one the wings were considerably shortened, though they were still functional; in another, the wings were greatly reduced and of abnormal shape, so as to be useless for flight; in still another the wings were inflated like a balloon; in a fourth, wings were practically wanting. The body color, normally a

brownish gray, has changed to yellow and black. Additional bristles on the body and bristles forked at the end are other new features. Besides these, there are a number of physiological changes not detectible by morphological means, but easily demonstrated by breeding experiments. Almost four hundred mutations of all kinds have been detected. All these new features are inherited. All of them therefore exemplify the process of evolution. Some of these mutations closely parallel changes that have evidently occurred in wild flies, showing natural evolution to be like that which occurs in captivity; and some of the modifications (in bristle characters, for example) concern features used in the classification of flies in nature. Furthermore, new characters arising in nature have not always been advantageous. The question whether the individuals possessing the new characters would have survived if they had

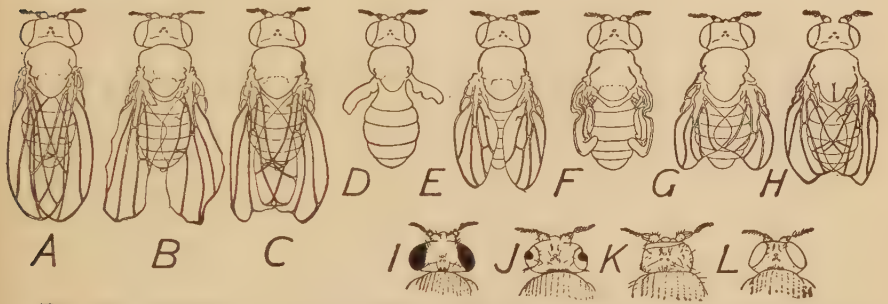

FIG. 257.—Mutations in the fruit fly *Drosophila melanogaster*. *A*, normal wing; *B* beaded wing; *C*, notch wing; *D*, vestigial wing; *E*, miniature wing; *F*, club wing; *G*, rudimentary wing; *H*, truncate wing; *I*, normal red eye; *J*, bar eye; *K*, eyeless; *L*, white eye. (*C from Morgan; D and L original; the rest from Morgan, Sturtevant, Muller and Bridges, courtesy of Henry Holt and Company.*)

occurred wild instead of in a laboratory is of no importance in this connection. Survival would be of importance in deciding what kind of animals would be left after evolution had been taking place for a time. Survival must be taken into account in explaining the species alive on the earth today, for without doubt millions of evolutionary changes have taken place without leaving a trace either in living animals or in the fossils of past animals. But a change which is temporary, merely because the only individuals which possess it perish, is not for that reason without the pale of evolution. All that is required is that the new character be one which will be, in case of its possessor's survival, transmitted to its progeny.

Other organisms furnish equally good examples of mutations. The evening primrose, Œnothera, is every year producing new forms. Seeds of plants that have been self-fertilized, and whose ancestors have been self-fertilized for generations, and which should therefore be genetically nearly pure, give rise to plants strikingly unlike their parents in certain

features. These alterations affect the size of the flowers; the shape, size and arrangement of the buds; the size and distribution of the seed capsules (Fig. 258); the size and habit of growth of the whole plant (Fig. 259); the shape of the leaves; the color of the stems; the form of the leaf-rosettes of young plants (Fig. 260); and so on. These new characters have been regarded as mutations, for they are inherited. It is true,

FIG. 258.—Mutation in Œnothera involving the length of the seed capsule. The two specimens at the left are *Œnothera Reynoldsii* mutation *debilis*, a form which gives rise by mutation to the form represented by the two figures at the right, *Œnothera Reynoldsii* mutation *bilonga*. (*Photograph by Prof. H H. Bartlett.*)

they are not inherited in quite the way that Mendel's law would lead one to expect. Œnothera is a peculiar organism in this regard. Inheritance in the evening primrose is governed by a number of special conditions, which make it an unsatisfactory organism for a first study of heredity; nevertheless the new traits mentioned above are inherited. The new characters are therefore commonly regarded as mutations, although

some biologists conceive the evening primrose to be a very complex heterozygote, and the new forms annually arising to be the results of recombination in the F_2, F_3.....F_{50}.....F_n.....generations. At least one of the mutations of Œnothera is known *not* to be the result of recombination, for the mechanism of mutation has been discovered. The form known as *Œnothera gigas* owes its origin to the doubling of the number of chromosomes, and cannot therefore be attributed to recombination of the traits of a hybrid parent.

Mutations are likewise known in other plants, in mice, and in guinea pigs. These organisms are specifically named as having given rise to

FIG. 259.—Mutation in Œnothera involving habit of growth. At the left, *Œnothera pratincola*, from which have arisen by mutation *Œnothera pratincola* mutation *latifolia* (middle) and *Œnothera pratincola* mutation *formosa* (right). (*Photograph by Prof. H. H. Bartlett.*)

mutations, because they have been extensively bred under critical observation. Other animals and plants, found in nature with unusual characters, are believed to have mutated, but it is only in cases where the ancestry is known for a number of generations that one can be reasonably certain that a new character is a mutation. The occurrence of well authenticated mutations in a few organisms, and in considerable numbers, renders the assumption of mutations in doubtful cases at least probable.

What Evolution Explains.—While direct observation of a process when it is occurring is the best possible evidence of that process, any facts which such a process will explain constitute contributory evidence.

Many facts of biology are easily explained as due to evolution, but are almost inexplicable on any other assumption. These facts come from various fields, of which comparative anatomy is one of the richest.

Comparative Anatomy.—Thus, the similarity of structure in different animals, as revealed by the study of comparative anatomy, is precisely what would be expected if evolution occurred, but would be

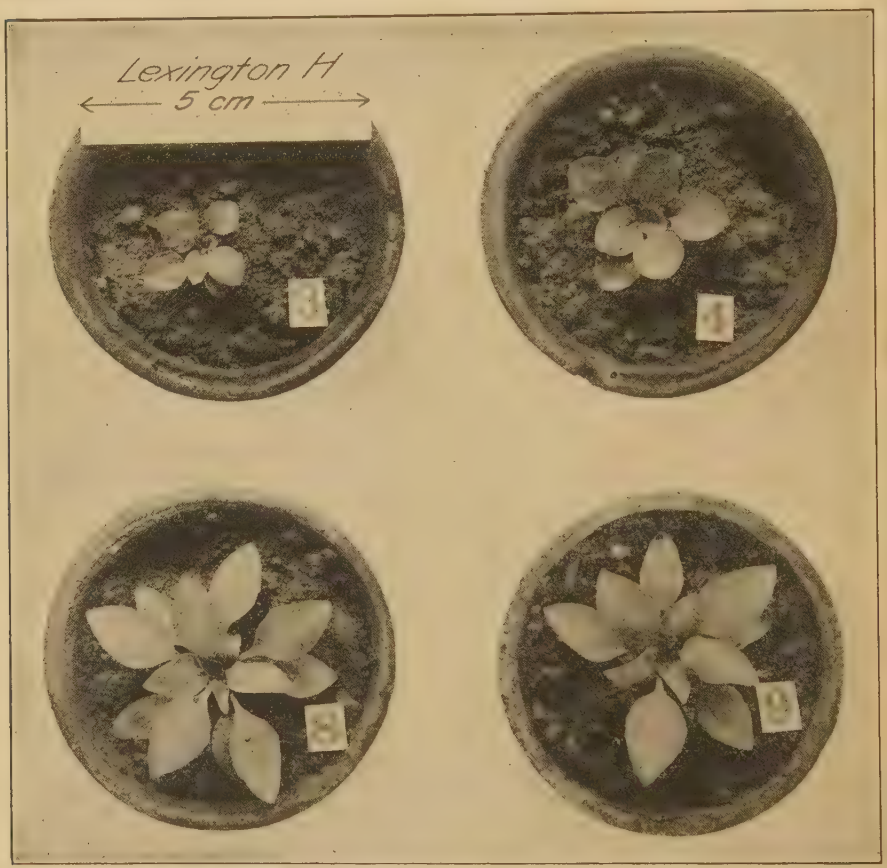

Fig. 260.—Mutation in Œnothera involving the rosettes, or young plants. Below (8 and 9) *Œnothera pratincola;* above (3 and 4) *Œnothera pratincola* mutation *nummularia*, a mutant of the preceding form. (*Photograph by Prof. H. H. Bartlett.*)

without meaning in the absence of evolution. The discovery of similar bones in the limbs of practically all vertebrates, though with modifications in each, can hardly mean anything else than that these animals have descended from common ancestors. The similarity of the labyrinth of the inner ear in various vertebrate animals (Fig. 261) is explicable on the same hypothesis. That is why homology is regarded as a certain sign of relationship. The differences found in homologous structures are

the results of evolution. The likenesses in homologous structures are the features not yet changed in diverse directions by evolution. In general very similar animals must be closely related; that is, their common ancestry dates from a comparatively recent time, so that there has been time for but a small amount of divergence by evolution. Very dissimilar animals which, however, have fundamental likenesses, must have diverged for a long time, that is, their common ancestors were very ancient.

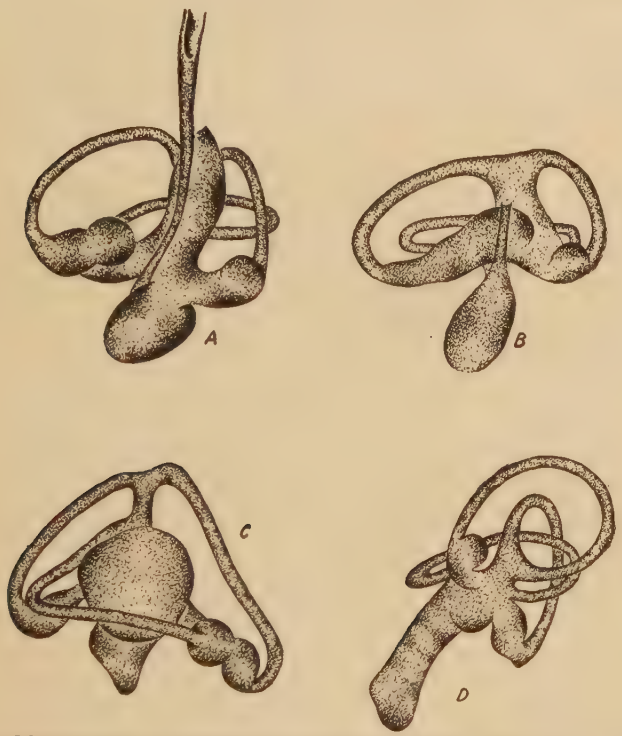

FIG. 261.—Membranous labyrinths of inner ear of various vertebrates. Each consists of a saccular portion from which three semicircular canals arise. These structures are homologous with one another, indicating relationship of the forms possessing them. *A*, of a fish; *B*, of a frog; *C*, of a reptile; *D*, of a bird. (*Modified from Retzius.*)

Comparative Embryology.—In similar manner, likenesses between the embryos of different animals are plausibly explained as due to common ancestry. Even in animals in which the adults are quite different, the embryos are sometimes similar. This is more often true in the case of parasitic animals, since adult parasites are frequently very degenerate. An excellent example of a case in which comparative embryology reveals common descent which the anatomy of the adult would not show is a parasite, Sacculina, found attached to the under side of the abdomen of common crabs (Fig. 262). Sacculina, in the adult stage, is a rounded pulpy mass with practically no definite structure, except a host of root-

like processes which extend throughout the crab's body and absorb the body fluids. The embryo, however, is a three-cornered little animal with jointed legs which clearly marks Sacculina as one of the Crustacea. It is, in fact, one of the barnacles, a group in which adult structure is usually quite complicated (Fig. 263). Its ancestors, if we may assume evolution to explain this case, were as highly developed as were other barnacles. but by a process of retrograde evolution it has become the degenerate mass of pulp that it is today. Comparative embryology also reveals, not only the fact of evolution, but the course of evolution in some cases. A case in point is the development of gill bars in the embryos of all vertebrate animals, whereas in only a few of the groups do adults have gills.

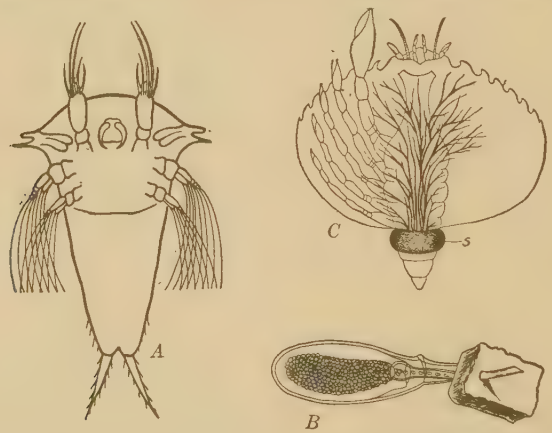

FIG. 262.—Sacculina, parasitic on crabs. *A*, young Sacculina, shortly after hatching, showing that its early development is like that of the Cirripedia (barnacles, etc.). *B*, young animal shown attached to its host, the crab. The projection at the anterior end has penetrated the chitinous ventral wall of the abdomen of the crab, only a small piece of the chitin being shown. Most of the early structure of the parasite is already lost. The mass of cells here shown subsequently passes through the tubular passage in front into the crab's body. *C*, adult Sacculina (*s*), consisting of a pulpy mass on the under side of the crab's abdomen, and a host of branching processes in the host's body. These processes absorb nutriment from the body fluids of the host. Practically all of the structure characteristic of the barnacles is lost. Magnification is not the same in the three figures. (*A and B after Delage.*)

Gill bars in the embryos not only reveal common ancestry, and hence a subsequent evolution, but also indicate that the common ancestors were fish-like animals—fish-like at least to the extent of having gills.

Comparative Physiology.—Similarities in physiological features are to be explained as a result of common descent, but known cases of this kind are less numerous than cases of morphological likeness, probably owing to the difficulty of discovering them. Animals whose blood compositions are very similar, as shown by the results of blood transfusions, are assumed to be closely related. At any rate, similar blood would be a result of common ancestry, and whatever differences now exist are the result of evolution. Fortunately, in general, animals shown by blood

tests to be closely related are also known by morphological similarities to have had recent common ancestry.

Extinct Animals.—The general relations of fossil animals to each other and to the geological formations are explained by evolution. The fact that, as one passes up through the stratified rocks, the animal remains gradually change, is precisely what evolution would require. The occurrence of fossils similar to living animals, but differing from them in some features, is no longer puzzling if evolution be assumed. Thus, as was pointed out in the preceding chapter, the early mastodons had long protruding faces, while the modern animals most resembling them, the elephants, have the front of the skull much flattened. Fortunately for the explanation of this difference, the later fossil mastodons had much shorter skulls than did the earlier ones. If the later forms evolved from the earlier ones, and if the shortening were continued down to the present time, there is no difficulty in accounting for the evident similarity of the mastodons and elephants in most respects. The differences in the teeth and lower jaw and proboscis and height of skull are explained in the same way. The mastodons and elephants are so much alike in general, that one is practically forced to regard them as members of the same line of descent. But if they are thus related, the form of the skull and the shape and number of the teeth and other features have been altered. The occurrence of horse-like animals in successive geological periods presents precisely the same problem. If the fossils of these animals be arranged in chronological order, there is so little difference between any one animal and those which immediately precede and follow it, that it is difficult to avoid the assumption that they were related to one another as ancestor and descendant. But if this be done, we must assume evolution.

FIG. 263.—Adult free-living barnacle of the genus Lepas, with half of its shell removed. The jointed appendages and some other features make it an arthropod. Its larva resembles that of Sacculina, Fig. 262, *A*. Compare the complex adult of Lepas with the degenerate adult of the parasitic Sacculina, Fig. 262, *C*.

Geographical Distribution.—Many phenomena of distribution which would be meaningless without the doctrine of evolution are entirely natural if modification occurred during descent. Along with the evolution of animals, it is often necessary to assume an evolution of the earth's surface, if the facts of animal distribution are to be made intelligible. Thus, the marsupials (pouched animals, including the opossum and kangaroo) are known to have existed since Mesozoic time. There are reasons for supposing that, at that time, Australia was connected with the American continent by a land bridge across the antarctic region, or indirectly through the other continents, or by both of these means. (See Fig. 264,

representing the connections just before the beginning of Mesozoic time, which continued partly through the Mesozoic.) As a result,

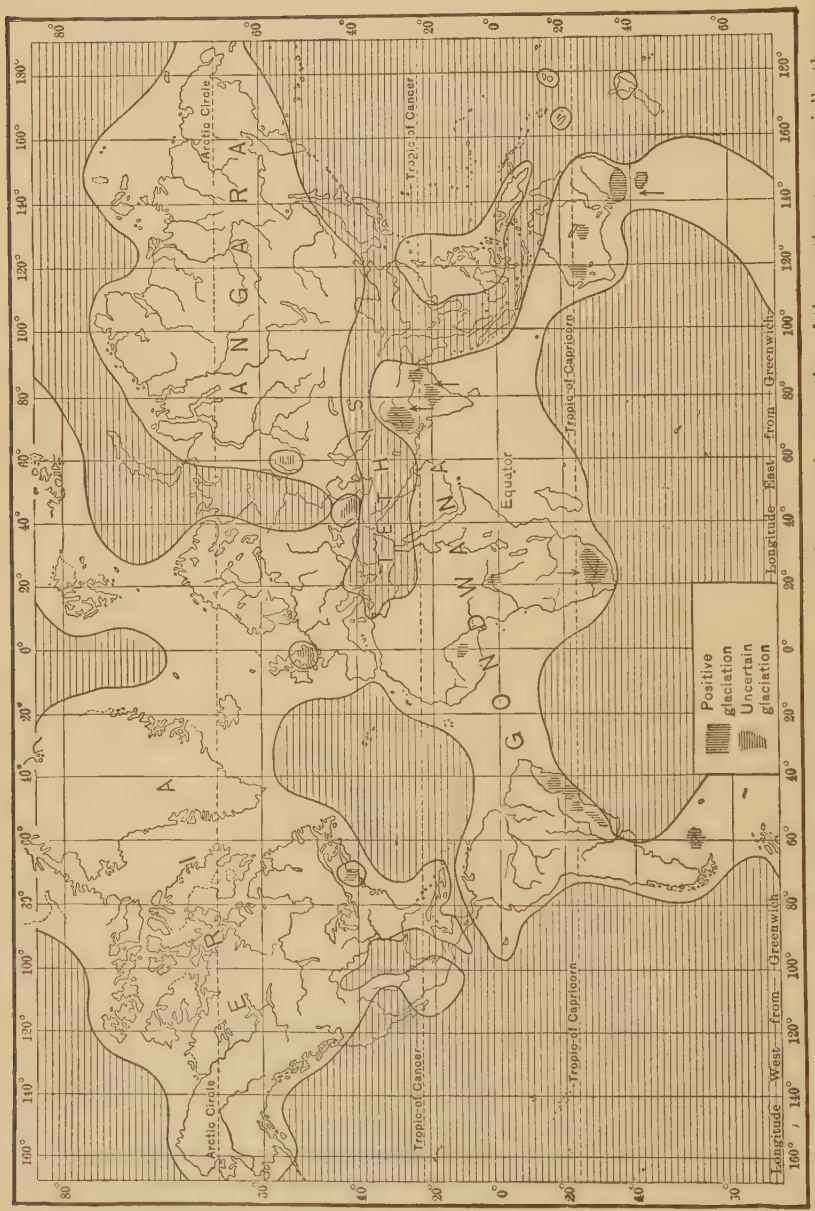

FIG. 264.—The geography of the world in early Permian time. Note the general connection of the continents, especially the union of Australia with the main continental mass. (*From Carnegie Institution of Washington and Schuchert's Historical Geology.*)

marsupials are found in both Australia and the Americas. But the marsupials of Australia and those of America are very different. If these fundamental likenesses, which make them all marsupials, indicate

a common ancestry, their differences require an explanation. Evolution offers that explanation. The ungulates (hoofed animals) do not

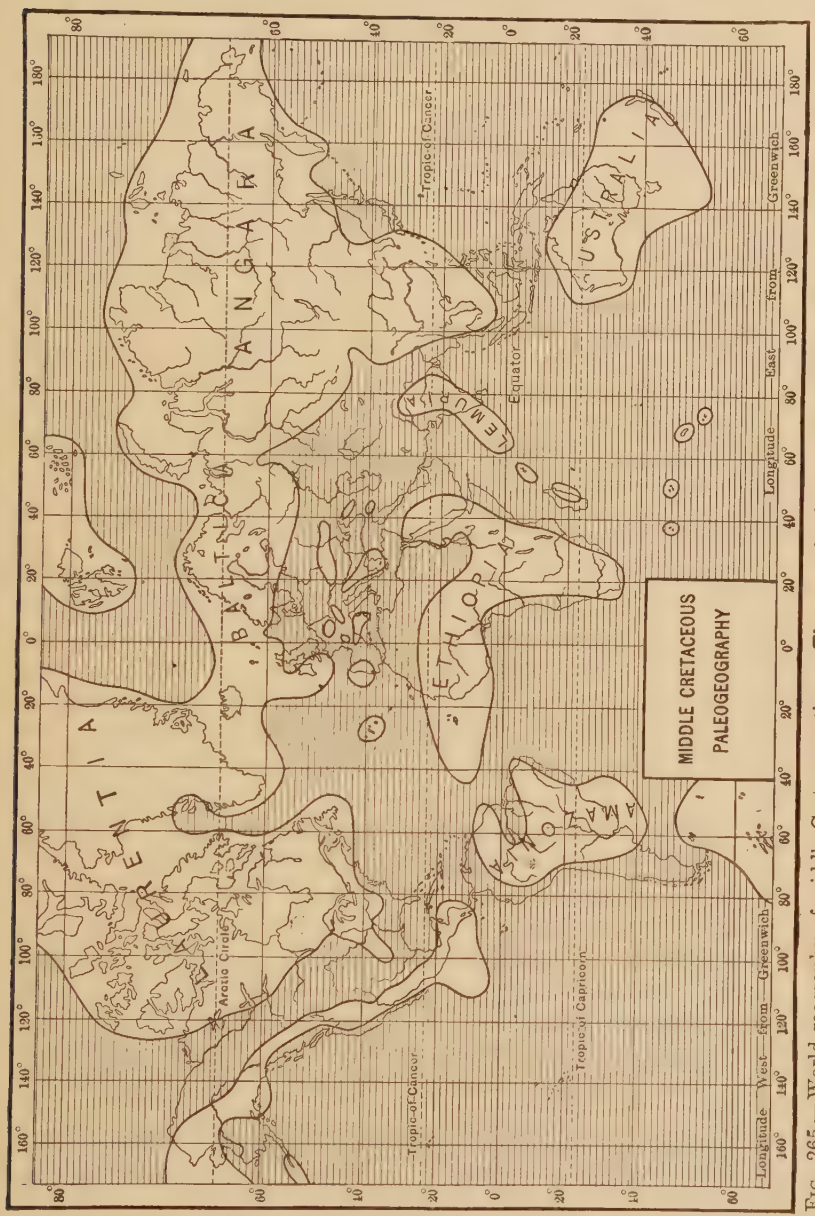

Fig. 265.—World geography of middle Cretaceous time. The great land mass is broken up into several continents. Note particularly the separation of Australia from other continents. (*From Schuchert's Historical Geology, John Wiley & Sons, Inc.*)

appear as fossils until after Mesozoic time, and until after Australia was separated from the other continents (Fig. 265). No ungulates are native to Australia. If ungulates came into existence in any other way than

by evolution from a common stock, there is no apparent reason why they should not have arisen in Australia. But if evolution be assumed as the only method of originating new forms, it is not difficult to understand why Australia never received representatives of this particular group. The ancestors lived elsewhere, and the migration of the descendants to Australia was barred by the sinking of the land.

The facts stated in the foregoing paragraphs, gathered from the provinces of comparative anatomy, embryology and physiology, from paleontology and distribution, receive a very simple and plausible explanation if evolution is assumed. These facts are only a few among a host that would have served equally well. Although these facts have not been specifically designated as evidence of evolution, they constitute such evidence. Facts which may be satisfactorily explained by a theory, and are not readily explained in any other way, are evidence in favor of that theory. To distinguish such evidence from that which comes from direct observation, it may be termed evidence by inference. The time was when inferential evidence was the chief, if not the only, kind advanced to support evolution. The doctrine of evolution was firmly established by evidence from paleontology, comparative anatomy, comparative embryology, and so on; for, at the time of the rise of the evolution theory, new characters had seldom been observed to arise among carefully pedigreed animals. Pedigrees were not common in the experiments of scientific men, and those kept by practical breeders were not always accurate in detail. Very few new characteristics had ever been observed at the time of their origin under circumstances which forbade their being attributed to hybridization or to the environment, until after the evolution theory had been generally accepted by biologists. The evidence which, as stated above, seems to us the best evidence, namely, the observation of mutations at the time of their origin, was not discovered in quantity until near the end of the last century, and since that time.

CAUSES OF EVOLUTION

While no thinking person now denies the fact of evolution, there is still much disagreement regarding the causes or method of the process. There are not wanting facts which bear on the question, but it is probable that a good many more facts are undiscovered or even undiscoverable. The question as to the causes of evolution must therefore be answered, if answered at all, in a rather speculative fashion. Before entering upon such speculation, it is essential to be perfectly clear as to what the problem is. As was pointed out early in the chapter, evolution occurs whenever a new character arises which is capable of being inherited. If it is clearly realized that, in discovering the causes of evolution, it is only the origin of mutations that is being considered, the discussion will be simplified. It matters not, in this connection, what kind of mutation

arises, nor whether the one or several animals which possess the new character survive or perish. These are questions which are discussed below under the caption *Course of Evolution*. Just now the thing requiring explanation is the origin of heritable changes.

Internal Factors: Mutations.—It has been indicated elsewhere that the characters of an animal are determined by something in the chromosomes of the germ cells from which the animal develops. Although individual characters may be impressed upon an organism by the environment, such features are rarely if ever, in the higher animals, handed on to the offspring. An evolutionary change must therefore presumably begin with a change in the chromosomes of the germ cells. What kind of change this must be is uncertain, for it is not clear what kinds of substances in the chromosomes are responsible for the development of hereditary traits. If the proteins determine development and heredity, a mutation may well result from a rearrangement of the atoms in the molecules. Proteins are very complex substances, their molecules being composed of hundreds or even thousands of atoms. No doubt, as in simpler organic compounds, these molecules have a definite configuration; that is, the proteins possess structure even when the chemist cannot discover it. In such complex bodies, by slight modifications, new molecules could be produced in which exactly the same atoms were present, but in different arrangement. Two or more substances whose molecules have the same number of atoms of each of the same elements, but differently arranged, are known as *isomers*. Isomers are known in many organic compounds, and they invariably differ from one another in some physical or chemical property. A substance may often be easily converted into one of its isomers, as for example, by the application of heat. If the proteins of the chromosomes should suffer any rearrangement of their parts, and their chemical properties be thereby altered, any hereditary traits determined by the modified proteins could hardly escape being different. Moreover, if the rearranged molecules were fairly stable, they would remain in the changed condition in succeeding generations, and the trait which they produced would be inherited. The altered condition would therefore be a mutation, a step in evolution. What sort of change in the adult would follow a given change in the proteins in the chromosomes could not be predicted. A shift of a few atoms to a new position, in the germ cells, might change the color of the eye or the shape of a bone. It is extremely unlikely that a molecular change of the kind hypothecated would not produce any alteration whatever in the adult. In view of the uncertainty regarding the nature of the material basis of heredity, further speculation of this kind would be unprofitable. If these paragraphs have shown what the problem of the cause of evolution is, and what sort of solution of it is to be expected, they have served their purpose.

Changes in the Environment.—Although environment is not generally accepted without reservations by leading biologists as an important cause of evolution, yet from its historical interest and from the belief still held by many biologists, it should be mentioned. Animals are often so obviously fitted for the environment in which they live, that observers are apt to conclude that in some way the environment worked them over until they were fit. Though it is not improbable that adaptation to environment is due to the migration of animals to that environment to which they are best fitted, provided they have had time to reach it and there is nothing in the way, environment as a cause of evolution cannot thus be swept aside without consideration. There are, as stated above, many biologists who firmly believe in the environment as an agent in bringing about evolution. That was Lamarck's view a century ago, and the same view is widely held today. As pointed out in the first chapter, some paleontologists, many medical men, and most of the laity are adherents, even now, of the Lamarckian theory. In support of their position may be cited the work of a few biologists who believe they have been able, in experiments, to produce by artificial means, such as changes of the medium, temperature, nutrition, or moisture, modifications which were subsequently inherited. In so far as these experiments have dealt with bacteria and other simple organisms, or the germ cells have been *directly* affected by the environment, the conclusions are in part apparently justified; but when they involved higher animals, and when the germ cells were not directly influenced, the experiments have never satisfied the majority of experimental biologists. Nevertheless it would be unfair to disregard these experiments. There is no *a priori* ground for supposing that environment could not effect evolution, and it may be that some day evidence so conclusive will be brought forth that everyone will admit its validity. That evidence, however, if it is ever secured, may easily prove unsatisfactory to those persons who most diligently seek it. For the strong appeal to the imagination made by the theory of environmental agency in evolution lies in the possibility that adaptation to environment may thereby be explained. It is well known that changes in the environment cause alterations in the bodies of animals and plants, and that some of these modifications are advantageous to the organisms. But in no case has it been established that one of these adaptive alterations has been transmitted to the descendants. Indeed, it is doubtful whether there exists in organisms any mechanism by which a purely somatic change could produce an effect on the germ plasm such that the *same* somatic character would appear in the next generation. The question whether the environment can produce permanent *adaptive* changes must be kept distinct from the question whether the environment may cause *evolution*. The latter question involves a smaller burden of proof than does the former.

Nothing here stated about the possible effect of environment, however, is in any way contradictory to the preceding paragraph about mutations and the chromosomes. For even if environment does produce heritable changes in organisms it is practically certain that the first effect wrought by the environment is a change in the chromatin, or whatever determines development and heredity. One could subscribe to the view that changes in the chromatin are the sole cause of mutations, and still go back one step farther and admit that the environment caused the alterations in the chromatin. Those who hold that environment has nothing to do with evolution regard the modifications of the chromatin as arising "spontaneously" from unknown causes within the animal.

COURSE OF EVOLUTION

Just as there has been confusion in the minds of writers and observers between the fact of evolution and the cause of evolution so has there been confusion between the cause of evolution and its course. It is important that these two matters be kept entirely distinct. One may discuss the direction in which species have become modified, without knowing or even caring why they became altered. Even by some biologists, those factors which guide evolution have been spoken of as if they started evolution. It is not inconceivable that the same agency both starts and directs evolution, but it need not do so. A projectile is thrown from a gun by the force of the explosion; but gravity determines the curve it decribes after leaving the muzzle. The engine and the steering wheel of a motor car are different things.

The Course of Evolution Demonstrated or Surmised.—Discussion of the course of evolution may involve one or both of two distinct questions. One is, what course has evolution taken? The other, what directed evolution in that course? The former question can be answered in part with considerable accuracy. So long as limited groups of animals are considered, it is often possible to determine relationships with a fair degree of certainty. There can be little doubt, for example, that the horse has descended from a five-toed ancestor of small size. The fossils show at least so much. They even show the order in which all toes except the third were reduced. Fossil cephalopods indicate that these animals changed from straight forms with straight septa to coiled forms, still with fairly straight septa; and that then the septa became bent and finally crinkled—in certain lines of descent. The shortening of the elephant's skull, the elongation and subsequent contration of the lower jaw, and the reduction in the number of the teeth, are likewise beyond doubt. Paleontology furnishes perhaps the best evidence of the course of evolution when the series of discovered fossils is fairly complete. But evidence as good as that concerning the horses and elephants is not common. To trace the lines of descent of animals whose ancestors are not abundantly

represented among known fossils, reliance is placed on comparative anatomy, comparative embryology, and geographical distribution. In erecting a family tree upon the basis of facts furnished by these sciences there is, however, much uncertainty. It is not difficult, in most cases, to decide what animals have descended from a common ancestor. When two species of garter snake differ only or principally in the number of rows of scales, they may safely be regarded as having been produced from the same stock. But was the ancestral species like the one modern species, or like the other? Or was it different from both? In answering such questions the zoölogist applies certain rules which seem to him to express probabilities. These rules may depend upon the amount of variability in the character which distinguishes the present species or the present distribution of these and other similar species. But any conclusion based on such rules is subject to risk, and the merits of each case have to be decided separately. In tracing the descent of the larger groups, still greater uncertainty exists. As pointed out above, the vertebrates have plainly come from a gill-bearing animal. But what are the steps by which the present condition, especially in those classes in which gills no longer occur (reptiles, birds, mammals), has been attained? Here opinion differs, and there has been much controversy over questions concerning the mutual relationships and intermediate stages of descent of these groups. When the biologist grows still bolder, and attempts to go back of the ancestors of the phylum, tracing the course of evolution is practically without foundation. It has been held probable, for example, that the annelids and arthropods have descended from common ancestors, partly because the members of both these phyla are segmented. But of the steps in the divergence of the two groups, if they really are related, there is almost no evidence whatever. Tracing such supposed pedigrees was fashionable among zoölogists during the latter third of the nineteenth century, until it was realized how speculative is the process.

Factors Directing the Course of Evolution.—Ideas regarding the agencies that guide evolution are as old as ideas of evolution itself. Speculation as to the reasons for the development of lines of descent is really older than the attempt to build family trees. Evolution was early thought of as a process of becoming perfect, whatever that might mean; and before this idea became concrete, and took the form of specific lines of descent, there was conjecture as to what led animals toward the goal of perfection.

Environment: Use and Disuse.—The early views of the guiding factors involved almost exclusively the environment and the effects of use and disuse. Both of these were embodied in Lamarck's theory of evolution. In some manner the environment was believed to be able to direct the changes, from generation to generation, in certain channels.

Lamarck speaks of the "needs" of the animal, or even of its "desire," becoming so great that the body responded by modifications in the required direction. Such a conception now seems to us, of course, the lightest of fancies. In similar manner the effects of use and disuse were believed by Lamarck to be inherited, and so to bring about modifications of the species. The stretching of the giraffe's neck after branches of trees, and the excessive use of the kangaroo's legs for jumping, he thought, caused an overdevelopment which was transmitted to their offspring. Although the increase in length of these organs was presumably small in any one individual, the accumulated increments amounted in time, Lamarck believed, to an enormous change. These views have been largely abandoned by the pure biologists, who realize that a blacksmith's children, if they are stronger than other children, are so because their father was inherently strong, and not because his occupation made him stronger. The strength of the blacksmith, which was his by inheritance, not trade, enabled him both to beget strong children and to follow a vocation requiring brawn. As stated in the first chapter, however, there are those, biologists among them, who still adhere to the Lamarckian view of the effects of use.

Natural Selection: Sexual Selection.—Darwin rejected, in the main, the Lamarckian principles, and proposed in their stead several forms of selection. The best known and the most generally applicable of his theories is that of natural selection which, indeed, is often called by the name "Darwinism." Animals, he said, naturally varied among themselves. If the variation of certain individuals was such as to give them a better chance in the struggle for existence, those individuals would survive in larger numbers than their less fortunate fellows, or would live longer and produce more offspring. Darwin assumed that, on the whole, the variations which helped these individuals would be transmitted to their progeny. In the next generation, he thought, the selection in favor of this variation would be repeated. In time, by this natural selection, a new race would be established. To explain such useless features as the gorgeous plumage of some kinds of male birds, features that could not help in the ordinary struggle for existence, Darwin postulated sexual selection. The more brilliant males, he thought, were more successful in courtship, and so left more progeny. Assuming variations in coloration to be inherited, a race having highly colored males would thus be evolved. In the hands of Darwin's followers and admirers the idea of selection was developed to an extraordinary degree. The most insignificant features were held to be an aid in the struggle for existence. One gained the idea, from following the arguments of these enthusiasts, that animals possessed no traits that were neutral or harmful, but that every structure and every habit was adapted to some use, and that the present existence of these structures and habits was due to their usefulness. It

is now known, however, that such useless or detrimental characters are not uncommon. Through no fault of Darwin's then, but because of the zeal of his apostles, the theory of natural selection came into a degree of neglect. Although careful breeding experiments indicate the effectiveness of artificial selection, there is no marked inclination among leading biologists to attribute to selection in nature, through the struggle for existence, anything but a purely negative rôle in evolution. Any modification that is very harmful would, of course, probably cause the death of its possessor. But characters that are neither useful nor harmful as well as those slightly harmful and those that are beneficial, might well be preserved. If the destruction of individuals in which very harmful new traits have appeared is all that natural selection accomplishes, it plays a much less important part in directing the course of evolution than Darwin (to say nothing of his more zealous and less discriminating followers) supposed.

Direction of Mutation.—Such negative action by natural selection could not, however, have been responsible for the course of evolution in the development of modern animals from their early ancestors. The direction of this great positive development, with little help or hindrance from natural selection, must have been due to something else. That other agency is believed to lie in the native internal capacity of protoplasm for undergoing change, or producing mutations, which was discussed among the causes of evolution but which must be alluded to here also as a factor determining the direction of evolution. Since mutations, as pointed out in the previous discussion, are probably the result of chemical changes of the chromatin, it will be seen that although a large number of such changes may be possible, there is a limit both to the number and to the kind of changes that may occur, and that the direction of evolution must be one or more of the directions of these possible changes. The kind of chemical change that occurs in a protein, for example, is strictly limited by the structure of its molecule. The kind of mutation that occurs, and hence the direction of evolution, is in turn dependent upon the kind of chemical change that is possible in the chromatin of the germ cells. The direction of evolution is therefore determined by the nature of the chromatin.

Orthogenesis.—What direction the changes in the chromatin, and hence the changes in the adult, will take cannot be foretold. It is possible that the molecular changes of the chromatin take place in a purely random manner. On the contrary, the shifting of the atoms in a particular manner at one time may make a further change of the same kind at a later time more probable. If the latter supposition is correct, and there are successive changes in the same direction in the chromatin of the germ cells, and if these changes produce, in the adult, modifications which are successively in the same direction, evolution proceeds as if

aimed at a definite goal. Cases in which successive steps in evolution appear to have been taken in the same direction are known. Such apparently directed evolution has been given the name *orthogenesis;* or, literally, development in a straight line. In orthogenesis the guidance of the evolution is held to come from within the organism, not from the environment. A case often cited in illustration is the development of the horse from a five-toed ancestor, through four-toed and three-toed ancestors, to the modern condition. Some paleontologists regard this particular case of straight-line development in the horse as being directed by the environment; but the view that it was internally guided is quite as tenable.

Orthogenesis is not to be assumed, however, in every case in which there is a graded series of forms. It must be known that these forms followed one another in proper order, from one extreme of the series to the other. A modern example will show how one might be mistaken in assuming orthogenesis where random mutation had really taken place. In the fruit fly, a large number of eye colors have originated in recent years. They range from a deep red to white, with the differences between some of the colors very slight. Some of the intermediate colors have been named cherry, pink, vermilion, eosin, buff, and tinged. If these colors be arranged in a graded series with red (the normal eye color of the wild fly) at one end and white at the other, they might be supposed to represent the successive steps in orthogenetic evolution, with white the final stage. This was not the order in which they arose, however, as white was the first to appear. Orthogenesis must not be accepted as demonstrated in a specific case, therefore, until the order of appearance of the various modifications is known, and until it is established that each member of the series was actually the ancestor of that which follows it. The case of toes in the horse lacks something of proof, as a case of orthogenesis, when judged by these criteria. The fossils show that, in general, the three-toed horses succeeded the five- and four-toed horses and were succeeded by the one-toed horse. It can only be inferred, however, that the three-toed horse descended from the four-toed, and gave rise to the one-toed. If this inference is correct, as it almost certainly is, there is only one other requirement. If the order in which the changes occurred was due to factors within the animals, and was not impressed by the environment, the gradual reduction of the toes of the horse from five to one is a genuine case of orthogenesis. Regarding the causation of these modifications opinions differ. Many biologists are of the opinion that they arose from internal agencies, independently of the environment.

Orthogenesis, if there is such a phenomenon, must not be regarded as an abstruse perfecting principle of any kind, but as being dependent on the chemical composition of the protoplasm. It is therefore to be expected that orthogenesis may occur in some animals, not in others.

Evolution by Hybridization.—Although new characters probably arise regularly in higher animals only by mutation, it is obvious that a form of evolution may take place by combination, in one organism, of features that have previously existed independently in different organisms. They are brought together in one individual by hybridization, producing combinations that did not exist before; for example, rough coat in guinea pigs may be combined with any of the coat colors. The combination is not always so simple as this, however, even where only two characters are involved. The bringing together in one animal of genes for two characters not previously combined sometimes produces a new character unlike either of those combined. A case of this kind

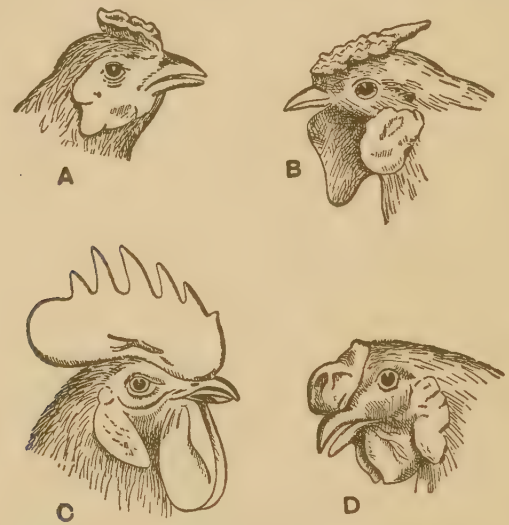

FIG. 266.—Combs in fowls. *A*, pea comb; *B*, rose comb; *C*, single comb; *D*, walnut comb. The walnut comb is a compound character, that is, it is produced by the coöperation of the factors for pea comb and rose comb. (*From Punnett's Mendelism, courtesy of The Macmillan Company.*)

has been described in the chapter on Genetics. Fowls with pea combs (small combs with a number of low prominences, Fig. 266), breed true to their form of comb. Rose comb (a low but thick comb with a roughened upper surface and a long tapering projection behind) is another true-breeding character. When a fowl homozygous for pea comb is mated with one homozygous for rose comb, the result is not a fowl having both pea and rose combs, but a new comb called walnut. This is a thick, fleshy, rounded comb overhanging the base of the beak. Other inherited features, requiring for their production the presence of half a dozen or more genes for simple characters, are known. The results of recombination through crossing cannot, therefore, always be foretold. The possibilities of evolution through hybridization are thus greatly

increased, and its range enormously widened. In view of these facts, it is not surprising that some biologists have regarded the new characters frequently arising in the fruit fly and the evening primrose as the result of recombinations of genes, and not as mutations at all. But, as pointed out before, even if this view should be correct, it would merely push back to an earlier time the production of the characters whose genes are supposed to be now shifting from one combination to another. For the various factors producing eye color in flies can hardly have existed in their present form from an indefinitely early time, even before flies had come into existence in the evolution of animals. They must have originated sometime in order to be recombined now, if this recombination is all that is happening. Their origin was probably the sort of chemical change which we call mutation.

Artificial Evolution.—The possibility of evolution through hybridization has been seized upon by man for his own advantage. The breeding of animals has occupied his attention in a commercial way for centuries and has resulted in striking improvements. But for a further statement regarding animal breeding the reader is referred to the chapter on Genetics. The attempt to bring about evolution by the artificial production of mutations has been attended with doubtful success. A few biologists, as pointed out above, believe they have altered the hereditary traits of animals by changing such features of the environment as temperature, nutrition and humidity; but their results have seldom been entirely satisfactory. The majority of biologists, on contemplation of their experiments, have usually been impelled to bring in the Scotch verdict of "not proven." Only one attempt to produce mutations by environmental means seems to have been eminently successful, namely, the experiments of Muller and others with Drosophila, using x-rays. Mutations of the kinds naturally appearing at intervals in these flies have been produced in these experiments in considerable numbers. Whether x-rays can be appealed to as a cause of evolution under natural conditions is uncertain.

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GLOSSARY

Pronunciations are indicated in the glossary as far as possible without the aid of diacritical marks, but the following symbols have been necessary:

H = the German ch;
N = the French nasal n;
ü = the French u, pronounced by shaping the lips for sounding long oo and the tongue for long ee.

Abiogenesis (*ab′ i o jen′ e sis*). The origin of living things from non-living matter; same as spontaneous generation. In its crude early form the belief that abiogenesis occurs has been abandoned.

Aboral. Opposite the mouth.

Absorption. The imbibing of a liquid by osmotic or capillary action.

Acanthocephala (*a kan′ tho sef′ a la*). A group of parasitic worm-like animals usually included with the Nemathelminthes. For definition see Chap. XIII.

Acetabulum (*as′ e tab′ u lum*). The socket on either side of the pelvic girdle for the head of the femur.

Actinian. A sea anemone.

Actinomorphes (*ak′ tin o mor′ feez*). A group of animals in Blainville's early classification; animals with radiating parts, such as the starfish.

Adaptation. Fitness for the environment. In a concrete sense, an adaptive structure, habit, or function.

Adductor. One of the large muscles attached to the valves of a mussel shell, or the corresponding muscle of a glochidium; also, one of numerous muscles in other animals which draw a structure toward the median axis.

Adipose. Pertaining to fat.

Adrenal. One of two or more ductless glands in close relation with the kidneys in most vertebrates.

Adsorption. The adherence of molecules of gases or dissolved substances to the surfaces of solid bodies.

Æolosoma (*e′ o lo so′ ma*). A genus of worms, phylum Annelida, subclass Oligochæta.

Aganides (*ag′ a ni′ deez*). A genus of extinct cephalopods with bent sutures of the goniatite form.

Agar (*ah′ gar*). A nutrient material used in bacterial cultures, etc.

Agassiz, Jean Louis Rodolphe (*ah′ gah see′*, Eng., *ag′ a see*). Swiss-American naturalist, 1807–1873.

Aggregation. A group of cells that have come together after having been previously apart from one another.

Agkistrodon piscivorus (*ag kis′ tro don pis siv′ o rus*). A species of snake, the cotton-mouth moccasin.

Alanine. One of the amino acids.

Albinism. The absence of the usual pigments in skin, hair, and eyes; said of individuals having white skin and hair and pink iris in species usually colored.

Albumen. A protein substance having certain properties, such as solubility in water, precipitability in strong acids, etc.

Alimentary. Pertaining to digestion or to the digestive tract.

Alternation of generations. See **metagenesis.**

Altricial (*al trish' al*). Hatched in a weak, helpless condition; said of certain birds.

Alveolar gland (*al ve' o ler*). A gland in which the lumen is inflated at certain points.

Amblycorypha (*am' bli kor' i fa*). A genus of katydids.

Ambulacral (*am' bu la' kral*). Resembling an alley; applied to the grooves beneath the arms of a starfish, in which the tube feet are located.

Ambystoma (*am bis' to ma*). A genus of salamanders. **A. maculatum,** a common species.

Amino acid (*am' i no*). One of a number of organic acids containing the NH_2 radical and having certain chemical properties. These acids enter into the composition of all proteins and are produced by the splitting of proteins.

Amino radical (*am' i no*). The radical NH_2 found in amino acids.

Amitosis (*a' mi to' sis*). Cell division not involving the formation of chromosomes or a spindle.

Ammonite (*am' mo nite*). An extinct cephalopod having a coiled shell and complicated foliaceous sutures; so-called from the genus **Ammonites.**

Amœba (*a me' ba*). A genus of one-celled animals, a protozoön of the class Rhizopoda. **A. diplomitotica** (*dip' lo mi tot' i ka*); **A. proteus** (*pro' te us*); **A. verrucosa** (*ver' ru ko' sa*).

Amœboid. Resembling Amœba; as, amœboid movement.

Amphiaster (*am' fi as' ter*). The figure produced by two asters and the connecting spindle in a dividing cell.

Amphibia. A class of Vertebrata embracing the frogs, toads, salamanders, and some others. For definition see Chap. XIII.

Amphicœlous (*am' fi see' lus*). Having both ends of the centrum concave; said of vertebræ.

Amphidisc (*am' fi disk*). Consisting of a rod with an expansion or disc at each end; said of sponge spicules.

Amphineura (*am' fi nu' ra*). A class of Mollusca, the members of which are bilaterally symmetrical, have a shell of eight pieces or no shell at all, and many pairs of gills. Chiton is an example.

Amphioxus. A primitive fish-like animal belonging to the subphylum Cephalochorda of the Chordata.

Amphiuma (*am' fi u' ma*). A genus of salamanders.

Amplexus. The clasping of a female by the male before or while the eggs are fertilized outside of the body, or while the spermatozoa are being deposited to be later secured by the female.

Amylolitic (*am' i lo lit' ik*). Carbohydrate-splitting.

Amylopsin (*am' i lop' sin*). A starch-digesting enzyme produced by the pancreas.

Anabolism. The aggregate of constructive processes comprised in metabolism.

Analogous (*an al' o gus*). Similar in function.

Anaphase (*an' a faze*). Any stage of cell division during the passage of the chromosomes from the middle to the ends of the spindle.

Anatomy. The science which treats of the structure of animals and plants as revealed by dissection. It more commonly deals with the grosser features, but the finest details of structure are not excluded.

Anaximander (*an aks' i man der*). A Greek physical philosopher and mathematician, pupil of Thales, who lived about 611-547 B.C.

Animal pole. That part of an egg in which the protoplasm is concentrated (in eggs with much yolk), and which in most animals produces the nervous system, sense organs, etc. Other features may also characterize the animal pole.

Anisogamy (*an' i sog' a mi*). Fusion of unlike gametes in reproduction.

Annelida (*an nel' i da*). The phylum of animals comprising the segmented worms. For definition see Chap. XIII.

Anodonta. A genus of freshwater mussels.

Antenna (*an ten′ na*) (*pl.*, **antennæ**). One of a pair of jointed appendages projecting forward from the head of an insect or crustacean.

Anthophysa (*an′ tho fi′ za*). A genus of colonial flagellate Protozoa whose cells are borne in radiating masses on a branching stalk.

Anthothrips niger (*an′ tho thrips ni′ jer*). A species of insect of the order Thysanoptera, commonly called thrips.

Anthozoa (*an′ tho zo′ a*). A class of Cœlenterata, comprising the sea anemones and most of the corals. They have no medusoid form in the life cycle.

Anthropoid (*an′ thro poid*). Man-like; said of certain apes.

Antirachitic. Serving to prevent rickets; said of a vitamine.

Antiscorbutic. Serving to prevent scurvy; said of a vitamine.

Ant-lion. An insect whose larva lives in a conical pit dug in the sand, capturing other insects that fall into the pit.

Anus (*a′ nus*). The posterior opening of the digestive tract.

Apoda (*ap′ o da*). An order of Amphibia comprising the legless forms called cœcilians.

Appendicular skeleton. The bones of the limbs and their attaching girdles in vertebrates.

Arachnida (*a rak′ ni da*). A class of Arthropoda comprising the spiders, scorpions, and mites. For definition see Chap. XIII.

Archæopteryx (*ar′ ke op′ ter iks*). An extinct animal of Jurassic time resembling both reptiles and birds, having teeth and feathers.

Archæozoic (*ar′ ke o zo′ ik*). Of the earliest geological period; the oldest known system of rocks is of this period.

Archenteron (*ark en′ ter on*). The cavity within the endoderm of a gastrula. It communicates with the exterior.

Archiannelida (*ar′ ki an nel′ i da*). A class of primitive marine worms (Annelida) without setæ.

Aristotle (*ar′ is tot′l*). The most famous of the Greek naturalist philosophers, who lived 384–322 B.C.

Armadillo. An armored mammal of the order Edentata, which includes also the sloths and ant-eaters.

Artery. A blood vessel conducting blood from the heart.

Arthropoda (*ar throp′ o da*). A phylum of animals, including the insects, crustacea, centipedes, etc. For definition see Chap. XIII.

Articulate. To join; said of bones.

Artificial parthenogenesis. The artificial stimulation of an egg to develop without fertilization.

Artiomorphes (*ar′ ti o mor′ feez*). A group of animals in Blainville's early classification; it comprised the animals whose bodies are bilaterally symmetrical.

Ascaris (*as′ ka ris*). A genus of roundworms (Nemathelminthes) parasitic in various animals. **A. megalocephala** (*meg′ a lo sef′ a la*), parasitic in the intestine of the horse.

Ascidian. Any one of a number of degenerate Chordata, members of the subphylum Tunicata, order Ascidiacea.

Asexual. Not involving germ cells nor fusion of nuclei; said of reproduction, or of an individual employing such a mode of reproduction.

Assimilation. The conversion of digested foods and other raw materials into protoplasmic substances.

Assortment. The distribution of genes of different pairs to the germ cells in maturation.

Aster. The star-like figure composed of a centrosome and the radiating lines about it; or the centrosome may be lacking.

Asteroidea (*as' te roi' de a*) A class of Echinodermata comprising the starfishes. For definition see Chap. XIII.

Astral rays. The radiating lines surrounding a centrosome in a dividing cell.

Asymmetrical. Not capable of being divided by a line or plane into halves which are mirrored images of each other.

Asymmetry. Absence of any kind of symmetry.

Auchenia (*aw ke' ni a*). The genus to which the llama and vicuna belong.

Auditory. Pertaining to hearing; applied to the nerve of hearing and the sensory part of the inner ear.

Auricle. The anterior chamber of the heart in fishes, and one of the two anterior chambers in higher vertebrates.

Autolytus (*aw tol' i tus*). A genus of marine worms.

Aves (*a' veez*). A class of vertebrate animals comprising the birds.

Avoiding reaction. The behavior by which Paramecium avoids obstacles of various kinds. It consists of stopping, moving backward, turning through an angle away from the oral groove, and starting forward in a new direction.

Axial skeleton. The skull, vertebral column, ribs, sternum, and hyoid apparatus of vertebrates.

Axolotl (*aks' o lot'l*). The larval form of the tiger salamander *Ambystoma tigrinum* which reproduces while in the larval state.

Axon (*aks' one*). A projection from a nerve cell which ordinarily conducts impulses away from the body of the cell.

Azotobacter (*a zo to bak' ter*). A genus of nitrogen-fixing bacteria.

Back cross. A cross between an F_1 individual and one of its parent types.

Balanoglossus. A genus of worm-like animals doubtfully included in the phylum Chordata.

Bascanion. A genus of snakes, including the black snake or blue racer.

Belon, Pierre (*be lon'*). French naturalist and traveler, 1517–1564.

Berengario (*ber' en gah' ri o*). Italian anatomist and surgeon in University of Bologna, in the sixteenth century.

Biconcave. Having the centrum hollow both in front and behind; said of vertebræ.

Bidder's canal. A longitudinal tube near the median border of the kidney of certain Amphibia; into it the collecting tubules open.

Bilateral symmetry. An arrangement of the parts of an object or animal body such that the halves on opposite sides of a certain plane (only one in number) are mirrored images of each other.

Bile. The fluid secreted by the liver in vertebrates.

Bile duct. The tube through which bile is discharged into the intestine.

Binomial. Consisting of two names or terms. Applied to the system of nomenclature by which each species is given two names, one for the genus, the other for the species.

Biogenetic law. The doctrine that animals in their embryonic development repeat the evolutionary history of the race.

Biology. The science of life and of living things, whether plants or animals.

Bionomics. The study of the relation of organisms to the environment.

Biota. The animals and plants of a given area or of a given period of time. (See **fauna** and **flora**, both of which are comprised under the term biota.)

Blainville, Henri Marie Ducrotay de (*blaN veel'*). French naturalist, 1777–1850.

Blastocœle (*blas' to seel*). The hollow interior of a blastula.

Blastophaga (*blas tof' a ga*). A genus of wasp-like insects of the order Hymenoptera, certain species of which dwell in figs.

Blastopore. The opening through which the archenteron of an early embryo (gastrula) communicates with the exterior.

Blastostyle. The central cellular core of a gonangium.

Blastula (*blas′ tu la*). An early developmental stage, consisting of a hollow ball of cells.

Blood platelet. One of the three general cellular components of the blood.

Bolina hydatina (*bo li′ na hi dat′ i na*). A species of ctenophore.

Book gill. See **book lung.**

Book lung. A respiratory organ composed of flat sheets joined together like pages of a book, found in spiders.

Bougainvillea ramosa (*boo′ gin vil′ le a*). A species of marine hydroid.

Bowman's capsule. The expanded end of a kidney tubule, in which a glomerulus is located.

Brachiopoda (*brak′ i op′ o da*). A group of marine animals of uncertain rank or relationship. They have a bivalve shell, the two halves of which are unequal. Sometimes placed in a phylum with the Bryozoa and Phoronidea.

Bract. One of the covering (protective?) members of a siphonophore colony.

Bradypus (*brad′ i pus*). A genus of sloths.

Branch. Any one of four major groups of animals in Cuvier's early classification.

Bronchus (*brong′kus*) (*pl.*, **bronchi**). One of the two main branches of the trachea in many vertebrates.

Brown, Robert. British botanist, 1773–1858.

Browse (*browz*). To eat the twigs of bushes or trees.

Bryozoa (*bri′ o zo′ a*). A group of marine and freshwater animals of uncertain rank and relationships, mostly colonial, bearing tentacles, and commonly known as moss animals. Sometimes placed in a phylum with the Phoronidea and Brachiopoda.

Buccal cavity (*buk′ k'l*). The most anterior division of the digestive tract of an earthworm. Also the mouth cavity of other animals.

Budding. Division of an organism into unequal parts in reproduction.

Buffon, Comte de (*bü foN′*). French naturalist, 1707–1788.

Bufo. A genus of toads.

Buprestis (*bu pres′ tis*). A genus of beetles.

Byssus. A thread attached near the adductor muscle of a glochidium; or a bunch of threads attached to the foot of certain clams.

Cæcum (*see′ kum*). The blind pouch at the beginning of the large intestine.

Calcarea. A class of sponges (Porifera) whose skeletons are composed of spicules of calcium carbonate.

Calorific (*kal′ o rif′ ik*). Heat-producing.

Cambrian (*kam′ bri an*). Of the earliest Paleozoic time.

Camelidæ (*ka mel′ i dee*). The family of camels.

Camelus (*ka me′ lus*). The genus of camels.

Camponotus. A genus of ants.

Canaliculus (*kan′ a lik′ u lus*). One of numerous minute channels radiating from each lacuna in the matrix of bone, in which slender processes of the bone cells are located.

Cancellate (*kan′ sel late*). Composed of a number of chambers separated by partitions; said of spongy bone.

Canine (*ka′ nine*). A tooth located laterally to the incisors.

Capillary. One of numerous small vessels conveying blood through the tissues from arteries to veins or from one vein to another.

Carapace. The hard bony covering of a turtle; also the chitinous or calcareous covering of the cephalothorax of a crayfish or lobster.

Carbohydrate. Any one of a class of organic substances, embracing the starches, sugars, cellulose, etc., which are composed of carbon, hydrogen, and oxygen, with the number of atoms of hydrogen and oxygen regularly in the ratio of 2 to 1.

Carboniferous. The geological age to which the principal known coal beds belong; late Paleozoic, succeeding the Devonian.

Carboxyl radical (*kar boks' il*). The radical COOH found in organic acids.

Carchesium (*kar ke' zi um*). A genus of colonial ciliated Protozoa, resembling Vorticella.

Cardiac. Pertaining to or near the heart.

Carettochelydidæ (*ka ret' to ke lid' i dee*). A family of turtles.

Carnivore. Technically, a mammal of the order Carnivora, including the cats, dogs, and seals. In a popular sense, any flesh-eating animal.

Carnivorous. Flesh-eating.

Carotin (*kar' o tin*). One of two yellow substances associated with chlorophyll.

Carpal. One of a number of bones in the wrist in vertebrates.

Carpometacarpus (*kar' po met a kar' pus*). A compound bone in the wing of a bird, formed by the union of several of the metacarpals and carpals.

Cartilage. A flexible somewhat translucent tissue composed of cells imbedded in a matrix, found on the ends of bones at joints and in other situations.

Cast. A mass of rock formed within a cavity, as the cavity of a shell or of a mold formerly occupied by an animal.

Catabolism (*ka tab' o liz'm*). The aggregate of destructive processes comprised in metabolism.

Catalysis (*ka tal' i sis*). A reaction produced by means of a catalyst.

Catalyst (*kat' a list*). A substance which brings about a reaction but is not consumed in that reaction. It probably often participates in the reaction, but is promptly reformed.

Caudal. Belonging to the tail.

Caudata. An order of Amphibia comprising forms with tails (salamanders, newts).

Cell. A mass of protoplasm containing a nucleus or nuclear material.

Cell doctrine. See **cell theory.**

Cell inclusions. Non-living objects enclosed in cells.

Cell membrane. A thin sheet either of differentiated protoplasm, or of some substance produced by protoplasm, surrounding a cell.

Cell theory. The theory that all animals and plants are composed of similar units of structure called cells. The theory is now so well established as to be more properly called the **cell doctrine,** and other features concerning physiology, development, etc., may be included in it.

Cellulose (*sel' u lose*). The substance, one of the carbohydrates, of which the cell walls of plants are commonly composed.

Cell wall. A non-living structure secreted by a cell around itself. It is commonly composed of cellulose or chitin.

Cement. A binding material in the composition of teeth.

Cemophora (*se mof' o ra*). A genus of snakes.

Cenozoic (*se' no zo' ik*). Pertaining to the most recent geological time prior to the Psychozoic.

Central nervous system. The brain and spinal cord.

Centriole. A minute body in the center of a centrosphere, and located at the end of the spindle of many dividing cells.

Centrolecithal (*sen' tro les' i thal*). Having the yolk in the central portion; said of eggs.

Centrosome (*sen' tro some*). A minute body often present in a cell, usually near the nucleus in a centrosphere, related in some way to the process of cell division.

Centrosphere (*sen' tro sfeer*). A differentiated portion of the cytoplasm of a cell, usually near the nucleus, and typically containing a centrosome or centriole.

Centrum. The massive portion of a vertebra ventral to the neural canal in which the spinal cord rests.

Cephalochorda (*sef' a lo kor' da*). A subphylum of Chordata, comprising the species of Amphioxus. For definition see Chap. XIII.

Cephalopod (*sef' a lo pod*). One of the group Cephalopoda, to which the cuttlefishes, squids, and nautili belong.

Cephalopoda (*sef' a lop' o da*). A class of Mollusca, comprising the octopi, squids, cuttlefishes, and nautili, animals in which the foot is developed into a head-like structure with eyes and a circle of arms.

Cephalothorax (*sef' a lo tho' raks*). A fused head and thorax, found in crayfishes and their allies.

Ceratite (*ser' a tite*). An extinct cephalopod having a coiled shell and crooked sutures; named from the genus Ceratites.

Ceratites (*ser' a ti' teez*). A genus of extinct cephalopods with crooked sutures; the common name ceratite is derived from this genus.

Ceratium candelabrum (*se ra' shi um can' de la' brum*). A species of protozoön which forms linear colonies.

Cerebellum. A division of the brain of vertebrates developed on the dorsal side anterior to the medulla.

Cerebrum. The anterior division of the brain in vertebrates. In man it forms the greater part of the brain, but is smaller in other vertebrates.

Cervical. Pertaining to the neck.

Cestoda. A class of Platyhelminthes, comprising the tapeworms. For definition see Chap. XIII.

Chætogaster (*ke' to gas' ter*). A genus of worms, phylum Annelida, subclass Oligochæta.

Chætognatha (*ke tog' na tha*). A group of marine animals of uncertain kinship, represented chiefly by the arrow worm Sagitta.

Chætopoda (*ke top' o da*). A class of worms (Annelida) provided with setæ, to which the earthworm and sandworm belong.

Cheloniidæ (*kel' o ni' i dee*). A family of turtles.

Chelydridæ (*ke lid' ri dee*). A family of turtles.

Chemotropism (*kem ot' ro piz'm*). The response of an organism to chemical substances.

Chitin (*ki' tin*). A horny substance forming the outside skeleton of insects and many other animal parts.

Chiton (*ki' ton*). A genus of primitive mollusks, having a shell of several pieces.

Chlamydomonas (*klam' i dom' o nas*). A genus of unicellular flagellate chlorophyll-bearing organisms.

Chloragogen cells (*klo' ra go' jen*). The cells of the outer layer of the intestine of the earthworm.

Chlorophyll. The green substance in chloroplasts through whose agency photosynthesis occurs.

Chloroplast. A green plastid.

Cholesterol (*ko les' ter ol*). A substance, one of the solid alcohols, found in many animal tissues.

Chondriosomes. Same as **mitochondria.**

Chordata (*kor da' ta*). A phylum of animals including the vertebrates and a few others. For definition see Chap. XIII.

Chromatin (*kro′ ma tin*). The deeply staining substance of the nucleus of a cell, attached to or embedded in the linin network.

Chromomere. One of the small aggregations of chromatin and other substances collectively forming a chromosome.

Chromoplast. One of several kinds of colored structures or organs found in many plant and some animal cells.

Chromosome. One of the rod-like or rounded bodies into which the chromatin of a nucleus is resolved at the time of cell division.

Chrysemys (*kris′ e mis*). A genus of turtles.

Chyme (*kime*). The fluid containing partly digested food found in the stomach.

Ciliary. Pertaining to cilia.

Ciliata. A class of the protozoa, in which both young and adult stages are provided with cilia.

Ciliate or ciliated. Provided with cilia.

Ciliophora (*sil′ i of′ o ra*). A subphylum of protozoa, members of which are covered with a pellicle, have a fixed mouth, and are usually covered with cilia; example, Paramecium.

Cilium. A minute hair-like motile structure occurring on the surface of certain cells.

Circular canal. A channel passing around a medusa near its margin.

Circulation. The movement of the blood through a system of vessels.

Circumpharyngeal connectives (*ser′ kum fa rin′ je al*). Nerve cords in the earthworm connecting the brain with the ventral nerve cord; so called because they pass around the anterior end of the pharynx.

Cirripedia (*seer′ i pee′ di a*). An order of Crustacea including the barnacles.

Cisco (*sis′ ko*). The lake herring.

Citellus tridecimlineatus (*si tel′ lus tri des′ im lin′ e a′ tus*). A species of ground squirrel.

Class. A subdivision of a phylum; a group of higher rank than the order.

Clavicle. The collar bone in man. One of the bones of the ventral part of the pectoral girdle in vertebrates in general.

Claviger (*klav′ i jer*). A genus of beetles.

Cleavage. The division or segmentation of an egg.

Clitellum. A thickened glandular band encircling the body of an earthworm.

Cloaca (*klo a′ ka*). A common passageway through which the intestine, kidneys, and sexual organs discharge their products in some fishes, in amphibia, reptiles and birds, and in a few mammals.

Cnidoblast (*ni′ do blast*). A cell containing a nematocyst or stinging thread in Hydra or other Cœlenterata.

Cnidocil (*ni′ do sil*). A trigger-like projection of a cnidoblast, by which the nematocyst is discharged.

Cocoon. A case in which eggs are stored and in which frequently the larvæ are developed; also a silky covering around the pupa.

Codosiga (*ko′ do si′ ga*). A genus of flagellate Protozoa having a collar around the flagellum.

Cœcilian. A legless Amphibian of the order Apoda.

Cœlenterata (*se len′ ter a′ ta*). The phylum to which Hydra, the hydroids, jellyfishes, and siphonophores belong. For definition see Chap XIII.

Cœlenteron (*se len′ ter on*). A cavity in forms like Hydra which have only one body cavity. It serves the digestive and circulatory functions and is therefore also called the gastrovascular cavity. It has only one opening.

Cœlom (*see′ lome*). The true body cavity, a cavity within the mesoderm on the walls of which the principal reproductive organs are located.

Cœnosarc (*se′ no sark*). The cellular living part of a hydroid, as distinguished from the perisarc.

Collared epithelium. Epithelium each of whose cells bears a collar.

Collecting tubule. One of a number of tubes leading across the kidney of the frog from Bidder's canal to the ureter.

Colloid (*kol′ loid*). A mixture in which particles invisible through a microscope but greater in size than molecules are held in suspension in a liquid.

Colloidal (*kol loi′ dal*). Contained in a liquid in aggregations submicroscopic in size but greater than molecules.

Colony. A group of individuals of the same species organically connected with each other.

Coluber. A genus of snakes.

Columnar epithelium. Epithelium in which the cells have one dimension distinctly greater than the others, that dimension being vertical to the surface covered by the epithelium.

Comanchian (*ko man′ chi an*). Pertaining to Mesozoic time prior to the Cretaceous; formerly called lower Cretaceous.

Commissure (*kom′ mi shure*). A group of connecting nerve fibers.

Common bile duct. The tube leading from the liver to the small intestine and serving to convey bile to the small intestine.

Compound gland. A branching gland.

Conchology (*kong kol′ o ji*). The zoölogy of the Mollusca

Conemaugh (*ko′ ne maw*). A rock formation of eastern United States, belonging to Permo-carboniferous time.

Coniferous. Cone-bearing (as pine or cypress trees).

Conjugation. The meeting of two cells for exchange of nuclear material or (by extension of meaning) for complete fusion.

Connective tissue. A tissue composed of cells and certain other material produced by the cells, which in its simple form binds organs and other tissues together. In a broader sense it includes such modified tissues as cartilage, bone, tendon, and ligaments.

Contractile tissue. Any tissue capable of active contraction; as muscle.

Contractile vacuole. A vacuole whose contents are periodically ejected to the outside of the cell in which it is contained.

Copepod (*ko′ pe pod*). Any one of a group of small Crustacea.

Copulation. The act of introducing spermatozoa into the body of the female.

Coracoid (*kor′ a koid*). A bone of the ventral part of the pectoral girdle of vertebrate animals; a distinct bone in the bony fishes, amphibia, reptiles, birds, and lowest mammals, but fused with the scapula in the higher mammals.

Cornea. The transparent bulging membrane at the front of the eye.

Corpora adiposa. Fat-bodies, storage places for reserve fatty food.

Corpuscle. One of the cells of the blood.

Cortex. The layer of gray matter which covers the cerebrum and dips into its folds. Also, an outer layer on various other organs.

Costiform. Rib-shaped.

Cranial nerve. One of ten or twelve pairs of nerves arising from the central nervous system within the skull.

Crepidula (*kre pid′ u la*). A genus of marine limpets allied to snails.

Cretaceous. Pertaining to late Mesozoic time; so named from the chalk deposits characteristic of it.

Crinoidea (*kri noi′ de a*). A class of Echinodermata, including the feather stars and sea lilies. For definition see Chap. XIII.

Cristatella mucedo (*kris ta tel′ la mu se′ do*). A species of freshwater bryozoön.

Crocodilini (*krok′ o di li′ ni*). An order of Reptilia comprising the alligators and crocodiles and their allies.

Crô-Magnon (*kro man′ yon*). A rather highly developed race of men preceding the principal races of today. It dwelt, as far as known, in western Europe.

Crop. In the earthworm, an enlargement of the digestive tract behind the esophagus and in front of the gizzard. In birds, an enlargement of the esophagus for the temporary storage of food.

Crustacea. A class of arthropods including the lobsters, crabs, water fleas, barnacles, etc. For definition see Chap. XIII.

Cryptobranchus (*krip′ to brang′ kus*). A genus of salamanders of large size.

Crystalline lens. A rounded, transparent, refractive body situated behind the pupil of the eye.

Ctenophora (*te nof′ o ra*). A phylum of animals including the comb jellies and sea walnuts. For definition see Chap. XIII.

Cubical epithelium. Epithelium in which the height and width of the cells are about equal.

Cuticle. Same as **pellicle.** Also same as **epidermis.**

Cuvier, Georges (*kü vyay′*). French naturalist, founder of comparative anatomy, 1769–1832.

Cyclosis (*si′ klo′ sis*). The rotation of protoplasm about the interior of a cell.

Cyclostomata (*si′klo sto′ ma ta*). A class of Vertebrata having an eel-like form, a cartilaginous skeleton, no jaws, and no lateral fins; lampreys and hagfishes.

Cyst. Any enveloping structure, usually a secreted membrane.

Cytoblastema (*si′ to blas′ te ma*). The name given to a supposed formative or nutri tive substance in organisms, from which cells were early thought to be formed.

Cytology. The science which deals with the structure of cells.

Cytoplasm. The protoplasm of a cell exclusive of the nucleus.

Dace. One of several small species of fish.

Darwin, Charles. Celebrated English naturalist, founder of the doctrine of natural selection, author of several works on evolution. Lived 1809–1882.

Darwin, Erasmus. English naturalist and poet, grandfather of Charles Darwin. Lived 1731–1802.

Darwinism. The theory of natural selection, propounded by Charles Darwin. (By the German biologists the term is often used to mean evolution.)

Deaminize. To remove the amino radical (NH_2) from; said of amino acids.

Deciduous. Falling off at maturity or at the end of a season; said of the leaves of trees which fall periodically. Applied also to trees whose leaves fall periodically.

Delamination. Splitting off; said of a layer of cells.

Demospongiæ (*de′ mo spun′ ji ee*). A class of Porifera (sponges). For definition see Chap. XIII.

Dendrite. A projection from a nerve cell which ordinarily conducts impulses toward the body of the cell.

Dendritic. Tree-like.

Denticulate. Finely notched or toothed.

Dentine. The dense bony substance composing the bulk of mammalian teeth.

Dermatemydidæ (*der′ ma te mid′ i dee*). A family of turtles.

Dermatome. A portion of the mesoderm adjoining the myotomes.

Dermatozoa (*der′ ma to zo′ a*). A group of animals (literally, the skin or touch animals) in Oken's early classification. It comprised the invertebrates.

Dero. A genus of worms, phylum Annelida, subclass Oligochæta.

Desmognathus (*dez mog′ na thus*). A genus of salamanders.

Devonian (*de vo′ ni an*). Of middle Paleozoic age, next following the Silurian.

Dextrin. Any one of several related carbohydrates derived by hydrolysis from starch; among them being erythrodextrin, achroödextrin and maltodextrin.

Dextrose. Glucose or grape sugar.

Diaphragm (*di′ a fram*). A partition; specifically, the partition between the thorax and abdomen of a mammal.

Diastase. An enzyme that decomposes starch.

Dichogamy (*di kog′ a mi*). The maturing of the male and female germ cells of a hermaphrodite at different times, thus preventing self-fertilization.

Dichotomous *di kot′ o mus*). Regularly dividing into two parts; said of branching in certain plants, also of a system of classification in which each group is divided into two parts.

Differentiation. The process of becoming structurally unlike, or of becoming heterogeneous. Also the condition of heterogeneity resulting from differentiation.

Diffusion. The spreading of the molecules of one substance among those of another.

Digestion. The conversion of food into soluble substances which may diffuse through protoplasm.

Dihybrid. The offspring of two parents differing in two characteristics.

Dinosaur (*di′ no sawr*). One of an order of extinct reptiles of Mesozoic time, mostly of large size.

Dicœcious (*di ee′ shus*). Having the male and female organs in separate individuals; said of species.

Diploblastic. Composed of two layers of cells.

Diploid (*dip′ loid*). Double; specifically, the double number of chromosomes found in the somatic cells, and in germ cells before maturation, in bisexual animals. *Cf.* **haploid.**

Diplozoön (*dip′ lo zo′ on*). A trematode worm parasitic on the gills of fishes.

Dipnoi (*dip′ no i*). A subclass of Pisces, fishes with an airbladder functioning as a lung; the lungfishes.

Division of labor. Distribution of functions among cells, or organs, or individuals.

Dominant. Receiving expression when only one determining gene is present, and in the presence of the gene for a contrasted recessive character; said of inherited characters that are exhibited by heterozygotes.

Donacia. A genus of aquatic beetles.

Dorsal. Pertaining to the back; hence, usually, upper.

Dorsal aorta. A large artery formed, in fishes, by the union of vessels coming from the gills, and passing backward in the dorsal region.

Dorsal root. The dorsal one of two roots by which a spinal nerve is connected with the spinal cord. Its fibers are sensory in function.

Double refraction. The separation of a beam of light into two rays as it passes through a refracting medium.

Drosophila (*dro sof′ i la*). A genus of flies, of which the fruitfly (**D. melanogaster,** *mel′ a no gas′ ter*) is a common species.

Dujardin, Felix (*dü zhar daN′*). French naturalist, 1801–1860.

Duodenum (*du′ o de′ num*). The first of three divisions of the small intestine.

Dutrochet, René Joachim Henri (*dü tro shay*). French physiologist, 1776–1847.

Dyad. A double body formed by the division of a tetrad into two parts. It may consist of two halves of the same chromosome or of two halves of different chromosomes.

Echinoderm (*e ki′ no derm*). One of the Echinodermata.

Echinodermata (*e ki′ no der′ ma ta*). The phylum of animals including the starfishes, sea urchins, sea cucumbers, brittle stars, etc. For definition see Chap. XIII.

Echinoidea (*ek′ i noi′ de a*). A class of Echinodermata, comprising the sea urchins, sand dollars, and heart urchins. For definition see Chap. XIII.

Ecology (*e kol′ o ji*). The branch of biology dealing with the relation of animals or plants to their environment.

Ectoderm. The outer layer of cells of a gastrula, or the representative of this layer in later stages.

Ectoparasite. A parasite that is attached to the outside of the body of its host.

Ectosarc. The outer layer of protoplasm in cells in which the outer and inner protoplasm differ distinctly in structure, as in Amœba.

Edaphosaurus (*e daf′ o saw′ rus*). An extinct lizard-like reptile bearing a spiny fin on its back, from Permo-carboniferous rocks of North America.

Elasmobranchii (*e laz′ mo brang′ ki i*). A class of Vertebrata comprising the sharks, skates, rays, torpedoes, and chimæras. For definition see Chap. XIII.

Electrolyte. A substance which in solution is capable of conducting an electric current and of being decomposed by the current.

Elephas (*el′ e fas*). A genus of animals including living elephants and their fossil relatives of Pleistocene time.

Elodea (*el′ o de′ a*). A genus of aquatic plants.

Embryo. An undeveloped animal while still in the egg membrane or in the maternal uterus.

Embryology. The science which deals with the development of the embryo, or young stages, of animals or plants.

Embryonic. Pertaining to an embryo.

Empedocles (*em ped′ o kleez*). Greek philosopher and poet, born in Sicily. Lived about 490–430 B.C.

Empirical formula. A formula stating merely the number of atoms of the various elements in a molecule of a chemical substance.

Emulsion. A mixture of two liquids or semiliquid substances, neither one soluble in the other, the one being in the form of separate droplets suspended in the other.

Emulsoid. A mixture consisting of a liquid in which are distributed particles of a liquid or semisolid substance which are exceedingly minute yet larger than molecules.

Emys (*em′ is*). A genus of turtles of the family Testudinidæ.

Enamel. The very hard, polished calcareous substance forming the surface layer or internal plates in the teeth of mammals.

Endocrine secretion. A secretion which must leave the gland by diffusion, not through a duct.

Endoderm. The inner layer of cells of a gastrula, or the representative of this layer in later stages.

Endosarc. The inner mass of protoplasm in cells in which the outer and inner protoplasm differ in structure.

Enterokinase (*en′ ter o ki′ nase*). An enzyme produced in the small intestine and serving to convert trypsinogen into trypsin.

Enteropneusta (*en′ te rop nu′ sta*). A subphylum of Chordata, worm-like animals, of which Balanoglossus and Cephalodiscus are representatives.

Entomology. The zoölogy of insects.

Entoparasite. A parasite that lives within the body of its host.

Enzyme (*en′ zime*). An organic substance which brings about a chemical reaction but is not consumed by that reaction. Probably it participates in the reaction, but is promptly restored.

Eocene (*e′ o seen*). Of the earliest Cenozoic and Tertiary time.

Eohippus (*e′ o hip′ pus*). The earliest known ancestor of the horse, an extinct animal of Eocene time.

Epidermis. The outer of the two principal layers of the skin. Also an outer layer of cells in general.

Epistylis (*ep′ i sti′ lis*). A genus of colonial ciliated Protozoa, resembling Vorticella. **E. flavicans** (*flav′ i kanz*), one of the species.

Epithelial. Pertaining to an epithelium; as, epithelial tissues or structures.

Epithelium. A layer of cells at the surface of a tissue or organ, or lining a cavity.

Epizoanthus. A genus of sea anemones.

Equation division. A division in which chromosomes divide, thereby producing two equal cells; said of one of the maturation divisions as contrasted with the reduction division.

Equatorial. In the plane of a great circle halfway between the poles; said of a cleavage plane of an egg. Also, in a middle position in other objects.

Equatorial plate. The flattened group of chromosomes on the middle of the spindle of a dividing cell.

Equus (*e′kwus*). A genus of animals including the living horse and some of its fossil relatives of Pliocene and Pleistocene time.

Erepsin (*e rep′ sin*). A proteolytic enzyme produced in the small intestine.

Ergosterol (*er gos′ ter ol*). A substance, chemically a solid alcohol, obtained from ergot, a fungus. On irradiation with ultra-violet it possesses strong antirachitic properties.

Erosion. The wearing away (of rocks) through the action of water and other agencies.

Erythrocyte (*er′ i thro site*). A red blood cell.

Erythrodextrin (*er′ i thro deks′ trin*). A carbohydrate obtained by hydrolysis of starch.

Esophagus (*e sof′ a gus*). In the earthworm, a narrow passage leading from the pharynx to the crop. In vertebrates, the passage between the pharynx and the stomach.

Eudorina elegans (*u′ do ri′ na*). A species of colonial chlorophyll-bearing organism whose cells are imbedded in a spherical jelly-like mass.

Euglena (*u gle′ na*). A genus of green flagellate Protozoa.

Eupagurus. A genus of crabs.

Eustachian tube (*u sta′ ki an*). A passage between the pharynx and the tympanum or middle ear.

Eutheria (*u the′ ri a*). A subclass of Mammalia comprising the viviparous mammals.

Eutrephoceras (*u′ tre fos′ er as*). A genus of extinct cephalopods resembling Nautilus.

Evagination. The folding of a layer of cells outward from an enclosed cavity.

Evolution. The gradual or sudden change of animals or plants through successive generations.

Evolve. To change; to undergo evolution.

Excretion. The elimination of waste substances. Also, a substance excreted.

Exhalent. Breathing out; applied to one of the siphons of a clam or mussel.

Exoskeleton. A skeleton on the outside of the body, as in the arthropods.

External respiration. The passage of oxygen from the surrounding air or water to the blood.

F_1 (*ef′ wun′*). An individual or generation of individuals resulting from the crossing of two unlike parents. An abbreviation of the words *first filial.*

F_2 (*ef′ too′*). An individual or generation of individuals resulting from the mating of two F_1 individuals as parents. An abbreviation of the words *second filial.*

F_3. An individual or generation of individuals whose parents are F_2 individuals from a previous cross.

Factor. Something in a germ cell or other cell which is responsible for a hereditary characteristic. Also called gene. In a general sense, factor means any agent or cause of any phenomenon.

Family. A taxonomic group of higher rank than the genus but below the order.
Fat. A compound of glycerol and one or more fatty acids.
Fatty acid. An organic acid entering into the composition of fats.
Fauna. Collectively, the animals of a given region or of a given period of time.
Femur. The single bone of the thigh in vertebrates above the fishes.
Feral. Escaped from domestication. Also, sometimes, wild.
Fertilization. The union of an egg with a spermatozoön, a process requisite, in the higher animals, to the development of the egg.
Fibril. One of the longitudinal contractile threads of a voluntary muscle cell.
Fibula (*fib′ u la*). The outer one of two bones in the lower leg of vertebrates except the fishes.
Fission. The division of an organism into two approximately equal parts; or, simply, division.
Fix. To convert into compounds; said of the action of certain bacteria on the nitrogen of the air.
Flagellar. Pertaining to flagella.
Flagellate (*flaj′ el late*). Possessing flagella, or pertaining to or performed by flagella. As a noun, a flagellate protozoön.
Flagellum (*pl.*, **flagella**). A long whip-like motile projection from a cell.
Flame cell. A cell having a hollow interior in which a bunch of vibratile cilia are located, forming part of a protonephridium.
Flemming, W. A German biologist.
Flora. The plants of a given area or of a given period of time, taken collectively.
Fluctuating variation. A modification of an organism which is not inherited, and which is presumably due to the environment in a broad sense.
Fluke. Any one of several species of trematode worms.
Foot. The basal muscular part of a clam or snail, variously modified in many other mollusks. Also the terminal part of a leg, the base of Hydra, etc.
Foraminal aperture (*fo ram′ i nal*) In a sponge gemmule, the opening in the shell through which the young sponge escapes when it begins to develop.
Formaldehyde (*for mal′ de hide*). A gas whose formula is HCHO.
Fossil. The remains, or other indication, of a prehistoric animal or plant.
Furcula (*fur′ ku la*). The wishbone of a bird, consisting of the fused clavicles of the two sides.

Galen. Famous Greek physician and anatomist, born about 130 A.D. His writings were long the highest authority in medical science.
Gall bladder. A pouch in which the bile secreted by the liver is stored.
Galvanotaxis (*gal′ van o tak′ sis*). An orientation of an organism with reference to the stimulus of an electric current.
Galvanotropism (*gal′ van ot′ ro piz′m*). The response of an organism to an electric current.
Gamboge (*gam′ boje*). A resinous substance.
Gamete (*gam′ eet*). A germ cell, or other cell which fuses with a second cell in reproduction.
Ganglion (*gang′ gli on*) (*pl.*, **ganglia**). A mass of nerve cell bodies, usually forming a thickening in the course of a nerve.
Gasterosteus (*gas′ ter os′ te us*). A genus of fishes, the sticklebacks.
Gastric. Pertaining to the stomach.
Gastrocnemius (*gas′ trok ne′ mi us*). A large muscle in the calf of the leg in vertebrate animals.
Gastropoda (*gas trop′ o da*). A class of Mollusca including the snails and slugs, mollusks whose bilateral symmetry is often obscured by a coiled body and shell.

Gastrovascular. Serving the functions of digestion and circulation.

Gastrovascular cavity. See **cœlenteron.**

Gastrula (*gas′ tru la*). An early developmental stage, formed from a blastula, commonly by the invagination of the vegetative pole of the latter. The gastrula consists of two layers of cells (ectoderm and endoderm) surrounding a cavity which communicates with the exterior.

Gastrulation. The formation of a two-layered embryo from a blastula, by invagination of the vegetative pole, by delamination, or otherwise.

Gelatin. A jelly-like substance obtained by boiling from cartilage, bone, tendon, ligament, connective tissue, etc.

Gemmule. A group of cells forming a reproductive body in freshwater sponges.

Gene. Something in a germ cell or other cell which is responsible for a hereditary characteristic. Also called factor.

Generic (*je ner′ ic*). Pertaining to a genus.

Genetics. The science of heredity, variation, sex determination, and related phenomena.

Genital. Concerned with reproduction.

Genus (*je′ nus*) (*pl.*, **genera,** *jen′ e ra*). A group of species having so many structural features alike that they must be regarded as having sprung from common ancestry; a group of lower rank than the family.

Geoffroy-Saint-Hilaire, Etienne (*zho frwa′ saN te lair′*). French naturalist, 1772–1844.

Geotaxis. An orientation of an organism with reference to the stimulus of gravity.

Geotropism (*je ot′ ro piz′m*). The response of an organism to the stimulus of gravity.

Gephyrea (*je feer′ i a*). A group of worm-like animals of doubtful rank and relationships. They have sometimes been referred to the Annelida.

Germ cell. A cell capable of reproduction, or of sharing in reproduction, as contrasted with the somatic or body cells which are sterile; or, more strictly, a reproductive cell that has undergone, or will undergo, or whose cell descendants will undergo, maturation before participating in reproduction.

Germinal. Relating to the germ cells; said of epithelium, for example.

Gill. A structure having a surface enlarged usually by branching or folding, which serves a respiratory function.

Gill bar. The tissue between two gill clefts.

Gill clef . One of several openings from the pharynx to the sides of the neck or head of a vertebrate embryo or adult; derived from a gill pouch. Also called gill slit.

Gill pouch. One of several evaginations from the sides of the anterior part of the digestive tract in the embryos of vertebrate animals. In some animals they break open to the outside, becoming gill clefts.

Gizzard. In the earthworm, a thick-walled portion of the alimentary tract behind the crop. In birds, the posterior muscular division of the stomach.

Glacial. Pertaining to glaciers, or to the period when glaciers were common in regions now temperate, namely, late Cenozoic time.

Gland. An organ whose function is the secretion of something to be used in, or ejected from, the body.

Glaucomys. A genus of flying squirrels.

Glenoid fossa. The cavity into which the head of the humerus fits.

Glochidium (*glo kid′ i um*). The young stage of a mussel, which becomes temporarily attached to fishes.

Glomerulus (*glo mer′ u lus*). A coil of blood capillaries at the end of each tubule in the kidney of a vertebrate animal.

Glossozoa (*glos′ so zo′ a*). A group of animals (literally tongue animals) in Oken's early classification. It comprised the fishes.

Glottis. A slit-like opening in the larynx at the anterior end of the trachea in vertebrates.

Glucose. Grape sugar.

Glycerol (*glis' er ole*). An alcohol entering into the composition of fats and having the empirical formula $C_3H_5(OH)_3$. Same as glycerin.

Glycogen (*gli' ko jen*). Animal starch; a common form of stored carbohydrate food in animal tissues.

Gmelin, Johann (*gma' lin*). German botanist, 1748–1804.

Goblet cell. A secreting cell containing a substance ready for secretion, and often having the shape of a goblet owing to the enclosed substance.

Golgi apparatus (*gole' jee*). A structure of various shapes, often a network, and of unknown function, found in many cells, usually near the nucleus.

Gomphoceran (*gom fos' er an*). Any extinct cephalopod resembling Gomphoceras, whose shell was short and wide.

Gonad (*go' nad*). An organ in which germ cells (either oögonia or spermatogonia) are produced or lodged.

Gonangium (*go nan' ji um*). An individual without tentacles in a typical hydroid, whose function is the production of medusæ.

Goniatite (*go' ni a tite*). An extinct cephalopod having a coiled shell and bent or angular sutures; so named from the genus **Goniatites** (*go' ni a ti' teez*).

Gonionemus (*go' ni o ne' mus*). A genus of jellyfishes.

Gonium. A genus of colonial flagellate organisms in which the cells are arranged in a flattened plate.

Gonoduct. A tube by which germ cells (either eggs or spermatozoa) are discharged from a gonad.

Gonophore. One of the reproductive members of a siphonophore colony.

Gonotheca. The tough sheath surrounding a gonangium.

Gopherus (*go' fer us*). A genus of turtles.

Grain. Small elevations on the leaves of tobacco, due to certain kinds of deposits within them.

Grantia. A genus of calcareous marine sponges.

Graptemys (*grap' te mis*). A genus of turtles of the family Testudinidæ.

Graze. To eat grass or similar herbage.

Gregaloid. Loosely adhering in an irregular mass.

Grew, Nehemiah. English botanist, 1641–1712.

Grouse. One of several species of birds of the family Phasianidæ, to which the quail, turkeys, ptarmigans, and prairie chickens also belong.

Guanaco (*gwah nah' ko*). A llama-like animal of South America.

Gullet. A tube leading from the posterior end of the oral groove in Paramecium to the interior of the cell.

Gustatory (*gus' ta to ri*). Pertaining to the sense of taste.

Habitat. The kind of place in which an organism lives.

Halysites (*hal' i si' teez*). A genus of extinct chain corals.

Haploid. Single; referring to the reduced number of chromosomes in the mature germ cells of bisexual animals. *Cf.* **diploid.**

Harvey, William. An English physician and physiologist who lived 1578–1657.

Head. An enlarged anterior portion. In animals, the part usually containing the principal nervous centers and sense organs. In a spermatozoön, the enlarged part consisting mostly of the nucleus.

Heidelberg. A city in Germany near which the remains of a man-like being (the Heidelberg man) were found.

Heliotaxis. An orientation of an organism with reference to the direction of light.

Heliotropism (*he' li ot' ro piz'm*). The response of an organism to the direction of light.

Helminthology (*hel' min thol' o ji*). The zoölogy of parasitic worms.

Helodrilus fœtidus (*he' lo dri' lus fet' i dus*). A species of annelid worm found in manure heaps.

Hemoglobin. A reddish protein contained in the red blood cells; also spelled hæmoglobin.

Herbivorous. Plant-eating.

Heredity. The occurrence, in organisms, of any qualities due to the nature of the protoplasm of which they are made.

Hermaphrodite. An organism possessing both male and female organs. Also (adjective), possessing the organs of both sexes.

Hermaphroditism. The state of being a hermaphrodite.

Herpetology (*her pe tol' o ji*). The zoölogy of reptiles and Amphibia.

Heteromita lens. A species of flagellate protozoön.

Heteromorphes (*het' er o mor' feez*). A group of animals in Blainville's early classification; animals of irregular form, mainly sponges and Protozoa.

Heterozygote. An organism to which its two parents have contributed unlike genes with respect to some inherited character, and which in turn produces two kinds of germ cells with respect to that character.

Heterozygous. Of the nature of a heterozygote.

Hexactinellida (*heks ak ti nel' li da*). A class of Porifera (sponges) whose spicules are composed of silica.

Hexiology (*heks' i ol' o ji*). The science of the relation of animals and plants to their environment; sometimes erroneously spelled hexicology.

Hipparion (*hip pa' ri on*). An extinct horse-like animal of Miocene and Pliocene time in North America and Europe.

Hippocampus (*hip' po kam' pus*). A genus of fishes of bizarre form resembling in part a horse's head.

Hirudinea (*hi' ru din' e a*). A class of Annelida comprising the leeches. For definition see Chap. XIII.

Histology. The science which deals with the structure of tissues.

Holothurioidea (*ho' lo thu' ri oi' de a*). A class of Echinodermata, comprising the sea cucumbers. For definition see Chap. XIII.

Homo. The genus of animals comprising man.

Homolecithal (*ho' mo les' i thal*). Having the yolk uniformly distributed throughout; said of eggs.

Homologous (*ho mol' o gus*). Originating in the same way in evolution and hence in the embryo; said of organs or structures.

Homology. Similarity of origin in evolution and hence in the embryo; applied to organs that arise in the same way.

Homozygote. An organism whose two parents contributed to it similar genes for some inherited character, and whose germ cells are therefore all alike with respect to that character.

Homozygous (*ho' mo zi' gus*). Of the nature of a homozygote.

Hooke, Robert. English natural philosopher and mathematician, 1635–1703.

Hooker, Sir Joseph Dalton. English botanist, 1817–1911.

Hormone (*hor' mo ne* or *hor' mone*). A secreted substance which stimulates activity in an organ.

Humerus. The single bone of the upper arm in Amphibia and the higher vertebrates.

Huxley, Thomas. English biologist and lecturer, 1825–1895.

Hybrid. The offspring of two parents unlike one another in some heritable character.

Hybridization. The process of crossing animals having unlike heritable characters, thereby producing animals possessing genes for the traits of both parents.

Hydra. A small tubular freshwater animal with tentacles and stinging organs, belonging to the phylum Cœlenterata. Two species are common, **H. oligactis** (*ol' i gak' tis*), and **H. viridissima** (*veer' i dis' si ma*).

Hydractinia. A genus of polymorphic hydroids.

Hydranth. A Hydra-like tentacle-bearing member of a hydroid colony.

Hydroid. A colonial cœlenterate, the individuals of which resemble Hydra in certain respects.

Hydrolysis (*hi drol' i sis*). A double chemical decomposition in which one of the substances consumed is water.

Hydrolyze. To undergo, or to subject to, hydrolysis.

Hydrorhiza (*hi' dro ri' za*). That part of a hydroid colony which is attached to the substratum.

Hydrotaxis. A response to moisture.

Hydrotheca. The tough transparent sheath surrounding a hydranth of a hydroid; an expansion of the perisarc.

Hydrotropism (*hi drot' ro piz'm*). The response of an organism to water, or moisture.

Hydrozoa. A class of Cœlenterata, including Hydra, the hydroids, jellyfishes and some corals. For definition see Chap. XIII.

Hyla. A genus of tree frogs.

Hyoid. A bone or group of bones or cartilages located at the base of the tongue or in a corresponding situation.

Hypertonicity (*hi' per to nis' i ti*). The presence of a greater osmotic pressure than normal; for example, in sea water to which salts have been added.

Hypodermis. An external layer of cells beneath a secreted cuticle, as in the earthworm and in insects and Crustacea.

Hypohippus. An extinct horse-like animal of Miocene time in North America.

Hypostome. A projection from the center of the circle of tentacles in Hydra or one of the hydroids. It is perforated by the mouth.

Hypotonicity (*hi' po to nis' i ti*). The presence of a lower osmotic pressure than normal; for example, in diluted sea water.

Ichneumon fly (*ik nu' mon*). One of a family of parasitic insects of the order Hymenoptera.

Ileum (*il' e um*). The last and usually longest of three divisions of the small intestine.

Ilium (*il' i um*) (*pl.*, **ilia**). The dorsal bone of the pelvic girdle in Amphibia and the higher vertebrates.

Incisor. One of the front cutting teeth of a mammal.

Incubation. The warming of eggs, resulting in acceleration of their development.

Ingestion. The taking in of food.

Inhalent. Breathing in; applied to one of the siphons of clams and mussels, to certain pores of sponges, and to other passages.

Innominate bone. The single bone formed by the fusion of three bones of the pelvic girdle in man. This name is not usually applied in the case of other vertebrates, though fusion of the bones of the girdle commonly occurs.

Insecta. A class of Arthropoda having one pair of antennæ, three pairs of legs, and tracheæ for respiration; the insects.

Insectivore. Technically, a mammal of the order Insectivora, including the moles, shrews, and hedgehogs. In a popular sense, any insect-eating animal.

Interdigitate. To dovetail together like the interlocked fingers of the two hands; said of adjoining environments when strips of each project out into the other.

Internal respiration. The transfer of oxygen from the blood to the surrounding cells; true respiration.

Internal secretion. A secretion poured directly into the blood without passing through ducts.
Intracellular. Within a cell.
Invagination. The folding of a layer of cells inward into a cavity.
Invert. To hydrolyze (a compound sugar) into a monosaccharide.
Invertase (*in ver′ tase*). An enzyme splitting cane sugar into glucose and fructose.
Ion. An atom or group of atoms bearing an electrical charge, formed by many substances on going into solution.
Ischium (*is′ ki um*) (*pl.*, **ischia**). The posterior of two ventrally located bones of the pelvic girdle of vertebrate animals above the fishes.
Isogamete (*i′ so gam′ eet*). One of two gametes of equal size which fuse in reproduction.
Isogamy (*i sog′ a mi*). Fusion of like gametes in reproduction.
Isomer. One of two or more chemical substances composed of the same elements, and of the same number of atoms of each element per molecule. Each substance is an isomer of the other(s).

Jejunum. The second of three divisions of the small intestine.
Jensen, Zacharias. Dutch inventor of the microscope about 1591.
Jugular vein. A large vein returning blood from the head.
Jurassic. Of middle Mesozoic age; named from rocks in the Jura mountains.

Karyokinesis (*ka′ ri o ki ne′ sis*). Same as **mitosis.**
Keratin. A substance forming the bulk of horn, hair, nails, etc.
Kidney. The chief organ for the excretion of nitrogenous wastes in most vertebrates. Also an excretory organ in certain other animals.
Kinosternidæ (*ki′ no ster′ ni dee*). A family of turtles.

Labial palp. One of two pairs of flattened organs beside the mouth of mussels.
Labyrinth. The inner ear of vertebrates.
Lactase. An enzyme of the small intestine whose function is the conversion of milk sugar (lactose) into dextrose and galactose.
Lacuna. A space in the matrix of bone which contains in life a bone cell.
Lamarck, Jean Baptiste, etc. Celebrated French naturalist and proponent of evolution, 1744–1829.
Lamella. A layer.
Lamprey. An eel-like animal of the class Cyclostomata.
Lampsilis (*lamp′ si lis*). A genus of freshwater mussels.
Large intestine. The enlarged portion of the digestive tract following the small intestine.
Larva. A free-living developmental stage of an animal in which certain adult organs are still lacking or in which organs are present that are lacking in the adult.
Larynx (*lar′ inks*). An enlargement of the anterior end of the trachea, in which the vocal cords are located.
Lateral fold. One of two ridges of skin along the back of certain species of frogs, extending lengthwise at either side.
Latreille, Pierre (approximately *lah tray′*). French zoölogist, 1762–1833.
Lecithin (*les′ i thin*). One of a number of lipoid substances common in egg yolk, nerve tissue, and other kinds of cells.
Leeuwenhoek, Antonius van (*lay′ ven hook*). Dutch naturalist and microscopist, 1632–1723.
Leiolopisma (*le′ yo lo piz′ ma*). A genus of skinks (lizards).

Lemming. A rodent of the family Muridæ, to which the rats, mice, and muskrats belong.

Lepas anatifera (*le' pas an' a tif' er a*). A species of barnacle (subclass Cirripedia of the Crustacea). The goose barnacle.

Lepisosteus (*lep' is os' te us*). A genus of fishes including the gar pike.

Leptinotarsa (*lep' tin o tar' sa*). A genus of leaf-eating beetles to which the common potato beetle belongs.

Leptodactylus (*lep' to dak' ti lus*). A genus of frogs.

Lernæopoda edwardsii (*ler' ne op' o da ed wardz' i i*). A copepod (Crustacea) parasitic on the gills of certain fishes.

Leucocyte. A white blood cell.

Levulose (*lev' u lose*). Fruit sugar.

Linear. Arranged in a line or row.

Lingula. A genus of brachiopods, a group of uncertain relationships.

Linkage. The occurrence of the genes for two or more hereditary characters in the same germ cell more frequently than the operations of chance would require.

Linnæus, Carolus (*lin ne' us*). See **Linné.**

Linné, Carl von (*lin nay'*). Swedish botanist and naturalist, author of the binomial system of nomenclature and an artificial classification of animals and plants, 1707–1778.

Lipase (*li' pase*). A fat-splitting enzyme.

Lipoid (*lip' oid*). One of a group of substances whose chemical and physical properties resemble those of fats.

Lipolytic. Fat-splitting.

Lister, Joseph. English surgeon, 1827–1912.

Liver. A gland which secretes bile and other substances.

Loxoceras (*loks os' er as*). A genus of extinct cephalopods of the orthocone type.

Lumbar. Pertaining to the loins, the region of the back posterior to the ribs.

Lumbriculus. A genus of Annelid worms.

Lumbricus terrestris (*lum bri' kus*). A species of earthworm.

Lung. A respiratory organ in the vertebrates.

Lycopod (*li' ko pod*). A club moss.

Lyell, Sir Charles. A British geologist, 1797–1875.

Lymnæa (*lim ne 'a*). A genus of snails.

Lymph. A clear fluid containing colorless cells found in lymph vessels. It is essentially blood without its red cells and somewhat diluted.

Lymphatic system. A system of vessels conveying lymph in vertebrates.

Lymph heart. One of a number of contractile chambers in the lymphatic system of lower vertebrates which by their pulsation propel the lymph.

Lymphocyte. A cell in the lymph.

Macromere. One of the larger cells of a cleaving egg, usually near the vegetative pole.

Macronucleus. The large nucleus in a cell or organism having two nuclei of unequal size.

Macrosiphum sanborni (*mak' ro si' fum*). A species of insect, one of the plant lice, living on chrysanthemum plants.

Malpighi, Marcello (*mahl pee' gee*). Italian anatomist, founder of microscopic anatomy, 1628–1694.

Malpighian corpuscle. One of numerous bodies in the kidneys of vertebrate animals, each composed of the expanded end of a kidney tubule (Bowman's capsule) and an enclosed knot of blood capillaries (glomerulus).

Maltase. An enzyme splitting maltose into glucose.

Malthus, Thomas Robert. English political economist, author (1803) of *Essay on Population*, who lived 1766–1834.

Maltose. Malt sugar.

Mammal. One of the Mammalia.

Mammalia. A class of vertebrates having hairy bodies, producing young within the body of the mother, and nourishing the young after birth with milk secreted by the mother.

Mammalogy. The zoölogy of mammals.

Mammoth. An elephant-like animal of prehistoric times.

Mantle. A sheet of tissue, typically quite thin, which secretes the shell in mollusks.

Mantle fibers. Fibers lying about the periphery of the spindle of a dividing cell and extending from the centrospheres to the chromosomes.

Manubrium (*ma nu′ bri um*). A projection from the center of the subumbrella of a medusa, corresponding to the hypostome of a hydranth, and bearing the mouth at its end.

Marginal bone. One of a ring of bones around the margin of the carapace of a turtle.

Marsupial. A mammal having a pouch in which the young are carried (for example, the opossum and the kangaroo). As an adjective, possessing a pouch; as the marsupial frog.

Mastigophora (*mas′ ti gof′ o ra*). A class of protozoa, characterized by flagella.

Mastodon (*mas′ to don*). An extinct genus of elephant-like animals of Pliocene and Pleistocene time.

Maternal. Pertaining to or derived from the mother.

Matrix. The non-cellular material in which the cells of bone and cartilage are imbedded.

Maturation. A process which germ cells undergo before they become functional, consisting essentially of (usually) two cell divisions, in at least one of which the behavior of the chromosomes is unlike that in other cell divisions.

Medulla oblongata. The enlargement of the anterior end of the spinal cord in vertebrates, commonly regarded as the posterior division of the brain.

Medusa (*pl.*, **medusæ**). A jellyfish; the free-swimming member of many hydroid species.

Megapodes (*meg′ a po′ deez*). Birds of the family Megapodiidæ, the mound birds and jungle fowls.

Mendel, Gregor. Austrian monk and plant breeder, founder of modern movement in genetics, and author of Mendel's Law of heredity. Lived 1822–1884.

Mendel's Law. The law that genes for inherited characters separate from one another and recombine in various ways in the germ cells.

Meridional (*me rid′ i o nal*). Passing through the animal and vegetative poles; said of certain cleavage planes of an egg.

Merychippus (*mer′ i kip′ pus*). An extinct horse-like animal of Miocene time.

Mesenchyme (*mes′ en kime*). A tissue composed of cells of irregular shape, loosely joined in a network with extensive meshes.

Mesentery (*mes′ en ter i*). A double sheet of tissue, continuous with the peritoneum, which supports an organ (such as the intestine) from the body wall.

Mesoderm. A layer of cells between the ectoderm and endoderm.

Mesoglœa (*mes′ o gle′ a*). The non-cellular layer between ectoderm and endoderm in Hydra and other cœlenterates.

Mesohippus. An extinct animal of Oligocene time, ancestral to the horse.

Mesothelium. The more compact portions of the mesoderm of an embryo, resembling epithelium.

Mesozoa. A group of degenerate animals of uncertain rank and relationship, once regarded as intermediate between protozoa and metazoa, hence the name.

Mesozoic. Pertaining to the geological era between the Paleozoic and Cenozoic, or the age of reptiles.

Metabolism (*me tab′ o liz′m*). The sum total of the chemical processes going on in protoplasm.

Metacarpal. One of the bones forming the body of the hand or fore foot in vertebrates.

Metagenesis. The occurrence of two or more forms of individual in the same species, one or more of which reproduce asexually and one of which reproduces sexually.

Metamere. See **somite.**

Metamerism (*me tam′ er iz′m*). The condition of being divided into a number of similar metameres or somites.

Metamorphosis (*met′ a mor′ fo sis*). The transformation of a larva into an adult.

Metaphase. That stage of cell division in which the chromosomes typically split. When the chromosomes do not split in the equatorial plate, there is difference in usage of the term.

Metatarsal. One of the bones forming the body of the (hind) foot of vertebrates.

Metatheria. A subclass of mammals including the marsupials or pouched mammals.

Metazoön. An animal composed of many cells. Although the term contrasts an animal with the protozoa, it is not a name of any taxonomic group of animals.

Miastor. A genus of flies; the larvæ are pædogenetic.

Microgromia socialis. A species of protozoön which forms a gregaloid colony in a gelatinous supporting substance.

Micromere. One of the smaller cells of a cleaving egg, usually near the animal pole.

Micronucleus. The smaller nucleus in a cell or organism having two nuclei of unequal size.

Micropyle. A small hole in the shell of an egg through which the spermatozoön enters in fertilization.

Microtus. A genus of field mice.

Mid-piece. A minute structure in a spermatozoön, between the head and the base of the tail.

Mimic. An animal which resembles another animal having some repellent or dangerous property which protects it.

Mimicry. The resemblance of one species to another, especially resemblance to one having some repellent or dangerous property.

Miocene. Belonging to middle Tertiary time; succeeding the Oligocene.

Mirbel, Charles Francois (*meer bel′*). French botanist, 1776–1854.

Mitochondria (*mi′ to kon′ dri a*). Objects of unknown function and of various shapes (thread-like, rod-shaped, or granular) found in the cytoplasm of many cells.

Mitosis. Cell division involving the formation of chromosomes, spindle fibers, etc. Also called karyokinesis.

Model. An animal with some protective property that is repellent or dangerous, to which another animal without such protective trait bears a resemblance.

Mœritherium (*me′ ri the′ ri um*). An extinct animal from the Eocene of Egypt, probably an early ancestor of the elephants.

Mohl, Hugo von (*mole*). German botanist, 1805–1872.

Molar. One of the grinding teeth of a mammal, back of the incisors and canines.

Mold. A cavity in a rock representing the form of an animal or plant or other object whose remains formerly occupied the cavity.

Molecule. Usually a group of atoms behaving as a unit of the substance which they compose. It is the smallest particle which possesses the chemical nature of the substance.

Mollusca. The phylum of animals including the clams, snails, cuttle-fishes, etc. For definition see Chap. XIII.

Mollusk. One of the Mollusca.

Molothrus (*mol' o thrus*). A genus of birds including the cowbirds.

Mondino da Luzzi (*mon dee' no da loot' see*). Italian anatomist in University of Bologna, in early part of fourteenth century.

Monocystis. A genus of gregarines, Protozoa of the class Sporozoa, order Gregarinida **M. agilis** (*aj' il is*) is a common species.

Monœcious (*mon ee' shus*). Having the organs of both sexes in the same individual which is thus a hermaphrodite; said of species.

Monohybrid. The offspring of two parents differing in only one characteristic.

Monotreme. One of the Monotremata (Prototheria); an egg-laying mammal having a cloaca.

Morphology. The branch of biology which deals with the structure of living things.

Motor. Pertaining to movement; applied to a neuron which conveys impulses resulting in muscular movement, glandular action, and the like.

Motor root. The ventral one of two roots by which a spinal nerve is connected with the spinal cord. So called because its fibers have a motor function.

Mucin (*mu' sin*). A substance from which mucus is derived; it is secreted by certain glands.

Mucosa. The layer of cells lining the digestive tract of vertebrate animals.

Muellerian duct (*mül le' ri an*). A tube formed in the embryo of most vertebrate animals, becoming the oviduct in the female and degenerating (with few exceptions) in the male.

Müller, Johannes (*mül' ler*). German physiologist and anatomist, 1801–1858.

Muscle. An aggregation of contractile cells.

Mustelus mustelus (*mus te' lus*). A species of shark.

Mutation. A heritable modification arising in an organism.

Mycelium (*pl.*, **mycelia**). The filamentous growths of fungi and related plants.

Myoneme. One of several contractile filaments in the stalks of Vorticella and its allies.

Myotome. One of the segments into which certain muscles are divided.

Myriapoda (*meer' i ap' o da*). A class of Arthropoda having tracheæ, one pair of antennæ, and many unspecialized legs; centipedes and millipedes

Myxomycetes (*miks' o mi see' teez*). The slime molds.

Nacre. The pearly substance secreted by mollusks upon their shell or other objects.

Nais. A genus of freshwater worms, phylum Annelida, subclass Oligochæta.

Nasal pit. The ectodermal depression in an embryo which forms much of the nostril.

Natrix. A genus of snakes. **N. rhombifera, N. sipedon,** two of the species.

Natural history. A descripitive account of things in nature, particularly animals and plants, though the term is sometimes used to include minerals, rocks, climate, etc.

Natural selection. The survival of the fittest individuals in the struggle for existence.

Nautiloid. One of the extinct cephalopods resembling Nautilus.

Nautilus. An animal belonging to the Cephalopoda, living in a coiled shell divided into chambers.

Neanderthal man (*na ahn' der tahl*). A man-like being whose remains have been found in various places in Europe.

Necator. The genus of roundworms to which the hookworm belongs.

Nectocalyx (*nek' to ka' liks*) (*pl.*, **nectocalyces,** *nek' to ka' li seez*). One of the swimming members of a siphonophore colony.

Necturus. A genus of salamanders; the mud puppies.

Nemathelminthes (*nem' a thel min' theez*). The phylum of roundworms and their allies. For definition see Chap. XIII.

Nematocyst (*nem′ a to sist*). One of the stinging bodies of Hydra and other cœlenterates.

Nematode (*nem′ a tode*). Any roundworm of the class Nematoda, phylum Nemathelminthes.

Nematomorpha (*nem′ a to mor′ fa*). A group of worm-like animals of uncertain affinities. They have usually been doubtfully included in the Nemathelminthes. For definition see Chap. XIII.

Nemertinea (*nem′ er tin′ e a*). A group of worm-like animals of uncertain relationships. They are regarded by some as a class of Platyhelminthes. For definition see Chap. XIII.

Nephridium (*ne frid′ i um*). An excretory organ of certain invertebrate animals (worms, mollusks, etc.), approximately corresponding in function to the kidney of vertebrates. It is commonly a coiled tube, as in the earthworm.

Nephrostome (*nef′ ro stome*). The opening at the inner end of a nephridium as in the earthworm. Also an opening (originally like that in the earthworm) connecting the cœlom with the blood vessels of the kidney in certain Amphibia.

Nereis. A genus of marine worms, phylum Annelida.

Neritina (*ner′ i ti′ na*). A genus of snails.

Nerve. A bundle of axons or dendrites of nerve cells or of both axons and dendrites.

Nervous tissue. Tissue capable of transmitting impulses; as the tissues of the brain, spinal cord and nerves.

Net-knot. A thickened portion of the chromatin of a cell nucleus.

Neural arch. That part of a vertebra above the centrum and neural canal.

Neural canal. The opening in a vertebra through which the spinal cord extends.

Neural crest. One of a number of groups of cells at the sides of the brain and spinal cord of an embryo, from which ganglia and nerves are developed.

Neural fold. One of the ridges of ectoderm forming the earliest development of the nervous system.

Neural groove. An elongated depression between the neural folds of an embryo.

Neural spine. A projection rising from the middle of the neural arch of a vertebra.

Neural tube. The tube formed beneath the ectoderm by the union of the neural folds along their crests.

Neuromuscular. Combining the functions of contraction and the transmission of impulses.

Neuron (*nu′ rone*). A nerve cell.

Nomenclature (*no′ men kla′ ture*). A system of naming; terminology.

Nostril. One of the external openings of the nasal chamber.

Notochord (*no′ to kord*). A cylindrical rod of cells beneath the nervous system of an embryo (adult of some animals). It is the forerunner of the spinal column of the vertebrate animals.

Notophthalmus (*no′ tof thal′ mus*). A genus of salamanders.

Nototrema. A genus of frogs.

Nuchal plate (*nu′ kal*). In turtles, the median plate of the carapace at the anterior end.

Nuclear membrane. A thin film of protoplasm surrounding the nucleus of a cell.

Nuclear sap. The liquid forming the bulk of the nucleus of a cell.

Nuclein. One of a number of protein compounds involving nucleic acid, found in abundance in cell nuclei.

Nucleolus (*nu kle′ o lus*). A small, usually rounded body found in the nuclei of many cells, which is of different chemical composition from the rest of the nucleus. Its function is uncertain.

Nucleus. A highly refractive, deeply staining body of specialized protoplasm found within nearly all cells.

Obelia. A genus of hydroids, or colonial Hydra-like animals of the phylum Cœlenterata.

Octopus. A genus of devilfishes (mollusks) having eight arms.

Œnothera (*e' no the' ra*). A genus of plants to which the evening primroses belong.

Oken, Lorenz. German naturalist and transcendentalist philosopher, 1779–1851.

Oleic (*o le' ik*). A fatty acid entering into the composition of olive oil.

Olfactory. Pertaining to the sense of smell.

Oligocene. Of early Tertiary time, between Eocene and Miocene.

Oligochæta (*ol' i go ke' ta*). A subclass of Chætopoda (Annelida), including chiefly terrestrial and freshwater worms with relatively few setæ which do not rest on fleshy outgrowths, but project directly from the body wall. The earthworm is an example.

Onychophora (*on' i kof' o ra*). A class of primitive Arthropoda having tracheæ and one pair of antennæ. Peripatus is an example.

Oöcyte (*o' o site*). A female germ cell subsequent to the initiation of maturation and prior to the second maturation division. An oöcyte is designated **primary** during the growth period and prior to the first division; **secondary** after the first division and before the second.

Oögensis (*o' o jen' e sis*). The maturation of female germ cells.

Oögonium (*o' o go' ni um*). One of the early germ cells of a female animal, prior to the beginning of maturation.

Oösperm (*o' o sperm*). A fertilized ovum; a term usually applied to plants rather than animals.

Opalina ranarum. A species of parasitic infusorian found in the intestine of the frog.

Operculum (*o per' ku lum*). A fold of skin covering the gills and gill clefts in some amphibian larvæ; also a similar covering of the gills in fishes.

Ophiuroidea (*o' fi u roi' de a*). A class of Echinodermata, comprising the brittle stars. For definition see Chap. XIII.

Ophthalmozoa (*of thal' mo zo' a*). A group of animals (literally eye animals) in Oken's early classification. The term was synonymous with Thricozoa, and comprised the mammals.

Opisthocœlous (*o pis tho see' lus*). Having the centrum concave behind and convex in front; said of vertebræ.

Optic nerve. The nerve of sight.

Oral groove. The spiral depression on one side of Paramecium, leading to the gullet.

Order. A group of animals forming a subdivision of a class, and being composed of one or more families.

Ordovician. Of early Paleozoic time, succeeding the Cambrian.

Organ. A group of cells or tissues performing some specific function.

Organism. A living being, whether plant or animal.

Organogeny. The embryonic origin of organs.

Ornithology. The zoölogy of birds.

Orohippus. One of the earliest known ancestors of the horse, an animal of Eocene time in North America.

Orthoceras (*or thos' er as*). A genus of extinct cephalopods of the orthocone type.

Orthocone. One of the early cephalopods that lived in a straight shell.

Orthogenesis. The repeated change of species in the same direction due to internal factors, and resulting in evolution in a "straight line."

Osmosis. The diffusion of a substance through a membrane in response to unequal distribution of that substance on opposite sides of the membrane.

Osmotic pressure. Objectively defined, the pressure that will just prevent diffusion of a solvent into a solution when the two are separated by a semipermeable

membrane. By some, however, regarded as the pressure due to the greater kinetic energy of the molecules of a solvent on one side of a semipermeable membrane than on the other, due to the presence of a solute on the side exhibiting the lesser kinetic energy of the solvent.

Otozoa. A group of animals (literally ear animals) in Oken's early classification. It comprised the birds.

Ovary. The organ in which the immature germ cells of a female animal are lodged.

Overgrowth. The growth of a layer of cells over underlying cells.

Oviduct. A tube through which the eggs of a female animal leave the ovary.

Oviparity. The condition of being oviparous.

Oviparous (*o vip′ a rus*). Egg-laying.

Oviposition. The laying of eggs.

Ovisac. A chamber for the storage of eggs, being in some cases a lateral pouch of the oviduct, as in the earthworm.

Ovoviviparity (*o′ vo viv′ i par′ i ti*). The condition of being ovoviviparous.

Ovoviviparous (*o′ vo vi vip′ a rus*). Producing young from eggs that are retained in the oviduct during their development, but without attachment to the oviduct, and wholly from nutrition stored in the egg.

Ovum. An egg; a relatively large passive cell which, in preparation for reproduction, has undergone one or two maturation divisions.

Oxidase. An enzyme which brings about oxidation.

Oxidation. The chemical process of combining with oxygen.

Oxyhemoglobin. Hemoglobin in combination with a certain amount of oxygen.

Pædogenesis (*pe′ do jen′ e sis*). Sexual maturity in an animal otherwise immature; the capability possessed by some species of reproducing while in the larval condition.

Palæomastodon (*pa′ le o mas′ to don*). A genus of extinct animals belonging to the elephant ancestry, found in the Oligocene of Egypt and India.

Paleobotany. The paleontology of plants.

Paleontology. The science which treats of prehistoric life on the earth, now represented by fossils.

Paleozoic (*pa′ le o zo′ ik*). Pertaining to the geological era prior to the Mesozoic, when Amphibia, fishes, and the higher invertebrates were the dominant forms.

Paleozoölogy. The science which deals with prehistoric animals.

Palmitic. One of the very common fatty acids.

Pancreas. A gland which secretes a fluid containing several digestive enzymes and discharges into the intestine.

Pandorina. A genus of colonial flagellate organisms in which the cells are held in a spheroidal jelly-like mass. **P. morum** (*mo′ rum*) is one of the species.

Papilio. A genus of butterflies; the swallowtails.

Paramecium. A genus of ciliated protozoa.

Parapodium. A fleshy lateral protrusion on the segments of some worms; it bears the setæ.

Parasite. An animal which lives in or on another species of animal (its host), at the expense of the latter.

Parasitism. The condition of being a parasite.

Parenchyma (*pa reng′ ki ma*). A loose spongy tissue found in certain low animals.

Parietal bone. One of a pair of bones on the posterior upper part of the skull of vertebrate animals.

Parrakeet. One of a number of small parrots.

Parthenogenesis (*par′ the no jen′ e sis*). The development of an egg without fertilization.

Parthenogonidia (*par' the no go nid' i a*). The asexually reproducing cells of Volvox.

Pasteur, Louis (*pas ter'*). French chemist and bacteriologist, 1822-1895.

Paternal. Pertaining to or derived from the father.

Pectoral girdle. A group of connected bones serving to attach the bones of the fore limbs of vertebrate animals to the rest of the skeleton.

Pelecypoda. A class of Mollusca having bivalve shells and a bilobed mantle; the clams and mussels.

Pellicle. A thin skin or film on the surface of a cell.

Pelvic girdle. A group of bones serving to join the bones of the hind limbs of vertebrate animals to the rest of the skeleton.

Penis. The copulatory organ in the male of many animals.

Pentadactyl (*pen' ta dak' til*). Having five fingers or toes.

Pepsin. An enzyme of the stomach of vertebrate animals, whose function is digestion of many kinds of protein.

Pepsinogen (*pep sin' o jen*). An inactive substance from which the enzyme pepsin is derived.

Peptic. Of the nature of pepsin; said of proteolytic enzymes that act in an acid medium.

Peptone. Any of a number of substances, derived by hydrolysis from proteins, which are not precipitated by ammonium sulphate.

Peranema (*per' a ne' ma*). A genus of colorless flagellate protozoa.

Pericardium. The membranous sac enclosing the heart.

Periodic. Occurring at rather regular intervals; said of migration which depends on the seasons or on the age of the migrating animals.

Perisarc. The tough sheath surrounding the stalk and branches of a hydroid.

Peritoneum (*per' i to ne' um*). A sheet of cells covering the viscera and lining the body cavity in many animals.

Permeable. Permitting the passage of both liquids and dissolved substances.

Permian. Belonging to the close of the Carboniferous age.

Petrifaction. The substitution of mineral matter for organic matter in the remains of animals or plants.

Phalanx (*fa' lanks*) (*pl.*, **phalanges,** *fa lan' jeez*). Any one of the bones of the fingers or toes in vertebrate animals.

Pharynx (*far' inks*). In an earthworm, the thick-walled portion of the digestive tract just posterior to the buccal pouch and in front of the esophagus. In vertebrates, the portion of the digestive tract at the back of the mouth, into which the gill clefts open.

Phoronidea (*fo' ro nid' e a*). A small group of marine animals, of which Phoronis is the only genus, of uncertain relationship to other animals. Sometimes placed in a phylum with the Bryozoa and Brachiopoda.

Photosynthesis. The construction of glucose from carbon dioxide and water by the energy of sunlight in the presence of chlorophyll.

Phototaxis (*fo' to taks' is*). A response to light.

Phototropism (*fo tot' ro piz'm*). The response of an organism to light.

Phylum. One of a dozen or more major groups into which the animal kingdom is divided; in general, the largest group of which it can be said that the members are related.

Physalia. A very complex colonial cœlenterate, one of the siphonophores.

Physiology. The branch of biology which deals with the functions of animals and plants, and the processes going on in them.

Piltdown. A locality in Sussex, England, near which primitive human fossils have been found.

Pineal body (*pin′ e al*). A structure on the dorsal side of the brain in vertebrate animals. Because of its similarity, in development, to the embryonic stages of an eye, it is often called the **pineal eye,** and is believed by many to be a vestigial sense organ.

Pinus. A genus of coniferous trees including the pines.

Pisces (*pis′ seez*). A class of vertebrate animals including the fishes. For definition see Chap. XIII.

Piscivore. A fish-eating animal.

Pithecanthropus (*pith′ e kan′ thro pus*). An extinct ape-like and man-like animal believed to be closely related to the early ancestry of man.

Pituitary (*pi tu′ i ta ri*). A glandular organ beneath the brain composed in part of nervous tissue.

Placenta. A vascular tissue dovetailing into the wall of the uterus on one side and connected with the umbilical cord on the other, thus forming an intimate nutritive connection between the embryo and the mother in viviparous animals.

Planaria. A genus of flatworms, phylum Platyhelminthes.

Planula (*plan′ u la*). A ciliated larva consisting of a solid ellipsoidal mass of cells, developed from the fertilized egg of a medusa or similar organism.

Plasma. The liquid part of the blood.

Plasmodium. The naked mass of protoplasm containing many nuclei, formed by the fusion of many amœboid cells in the Myxomycetes.

Plasmodroma. A subphylum of protozoa devoid of cilia.

Plastid. One of several kinds of protoplasmic bodies in cells, like the green bodies in plant cells, which are centers of chemical activity.

Plastron. The flat plate of bones on the ventral side of a turtle.

Plato. A Greek philosopher, pupil of Socrates and teacher of Aristotle. Lived about 427–347 B.C.

Platyhelminthes (*plat′ i hel min′ theez*). The phylum of flatworms. For definition see Chap. XIII.

Pleistocene (*plise′ to seen*). Belonging to the epoch following the Tertiary.

Pleodorina (*ple′ o do ri′ na*). A minute spherical organism composed of cells of two sizes embedded in a jelly-like substance. **P. californica** (*kal′ i for′ ni ka*), with numerous small cells; **P. illinoisensis** (*il′ li noi zen′ sis*), with four small cells.

Plethodon (*pleth′ o don*). A genus of salamanders.

Pliny (*plin′ i*). Roman naturalist (23–79 A.D.) and author of works on natural history.

Pliocene. Pertaining to the most recent epoch of Tertiary time.

Pliohippus. An extinct animal of Pliocene time, closely resembling the horse.

Pluvianus (*plu′ vi a′ nus*). A genus of birds.

Pneumatophore (*nu′ ma to fore*). A capsule enclosing gas, serving to float a siphonophore colony.

Poëbrotherium (*po′ e bro the′ ri um*). A genus of extinct animals resembling camels, recovered from the lower Oligocene.

Polar body. A small non-functional cell, one of the two cells produced by each division in the maturation of an egg.

Polarity. The condition of exhibiting or possessing different properties in different parts; the condition of a cell in which the protoplasm is unlike in different parts of the cell.

Pole. A differentiated part or extremity, as of an egg, or of the spindle of a dividing cell.

Polychæta (*pol′ i ke′ ta*). A subclass of Chætopoda (Annelida) including those marine worms having numerous setæ borne on fleshy outgrowths at the sides of the somites. Nereis, the sandworm, is an example.

Polymorphic. Having a variety of forms.

Polymorphism. The existence of two or more kinds of individuals within a species.

Polyorchis (*pol′ i or′ kis*). A genus of jellyfishes.

Polyp. One of the feeding individuals of a hydroid or coral colony or simple related form.

Polypeptide. A compound formed by the union of two or more molecules of amino acids with the loss of water.

Porcellio. A genus of sowbugs (Isopoda, Crustacea).

Porifera (*po rif′ er a*). The phylum of animals comprising the sponges. For definition see Chap. XIII.

Porocyte. A contractile cell in sponges, whose function is the contraction and expansion of the water pores.

Postcava. A large vein leading to the heart from behind or below.

Poterioceras (*po te′ ri os′ er as*). A genus of extinct cephalopods of the gomphoceran type.

Precocial. Able to run about as soon as hatched; said of certain birds.

Precoracoid. A ventrally situated bone or cartilage of the pectoral girdle in Amphibia and some reptiles.

Primary. For application to spermatocytes, see **spermatocyte.** For application to oöcytes, see **oöcyte.**

Primate. A mammal of the order including man and the ape-like animals.

Priority, Law of. The rule that the name first given a species along with a description is the one that shall be accepted when different names have been applied to the same species.

Proboscis (*pro bos′ sis*). The trunk of an elephant, consisting of the elongated nose and upper lip. Also a fleshy projection of other sorts.

Procœlous (*pro see′ lus*). Having the anterior end of the centrum concave, the posterior end convex; said of vertebræ.

Procyon (*pro′ si on*). The genus of Carnivora to which the raccoon belongs.

Proglottis (*pl.*, **proglottides,** *pro glot′ ti deez*). One of the individuals in a chain of a tapeworm.

Pronuba. A genus of moths some members of which feed on Yucca seeds.

Prophase. Any early stage of mitotic cell division, prior to the splitting of the chromosomes.

Prosecretin (*pro′ se kre′ tin*). A substance in the walls of the small intestine from which secretin is produced.

Prostomium. A rounded projection overhanging the mouth of an earthworm.

Protandrous. Maturing the male germ cells before the female cells; said of a hermaphrodite.

Protein. One of many organic substances, compounds of aminoacids, which therefore contain carbon, hydrogen, nitrogen and oxygen and often other elements. The molecules are large and very complex. Lean meat and egg albumen contain quantities of proteins.

Proteolytic (*pro′ te o lit′ ik*). Protein-splitting.

Proteose. Any one of a number of substances, derived from the hydrolysis of proteins, which may be precipitated from solution with ammonium sulphate.

Proterospongia hæckeli (*pro′ ter o spun′ ji a hek′ el i*). A species of protozoön which forms gregaloid colonies.

Proterozoic. Belonging to the era preceding the Paleozoic.

Proteus. A genus of salamanders.

Protogynous (*pro toj′ i nus*). Maturing the female germ cells before the male; said of hermaphrodites.

Protonephridium. A primitive excretory organ consisting of flame cells and connecting tubes.

Protophyta. Unicellular plants.

Protoplasm. The living matter of which animals and plants are essentially composed.

Prototheria. A subclass of Mammalia, including the egg-laying mammals such as the duckbill Ornithorhynchus and the spiny ant-eater Echidna.

Protozoa. One-celled animals. The phylum comprising the one-celled animals, including colonial forms in which the cells of the colony are, at least potentially, all alike.

Protozoölogy. The zoölogy of the protozoa.

Protylopus (*pro ti′ lo pus*). The earliest known ancestor of the camels.

Proventriculus (*pro′ ven trik′ u lus*). The first division of the stomach of a bird.

Pseudacris (*su dak′ ris*). A genus of frogs.

Pseudemys (*su′ de mis*). A genus of turtles of the family Testudinidæ.

Pseudopodium (*su′ do po′di um*) (*pl.*, **pseudopodia**). A blunt finger-like projection thrust out by Amœba and other rhizopods.

Psychozoic (*si′ ko zo′ ik*). Pertaining to the most recent geological time, that in which man developed as an intelligent being; the time following the Cenozoic era.

Ptyalin (*ti′ a lin*). The amylolitic enzyme of the saliva.

Pubis (*pl.*, **pubes**, *pu′ beez*). The anterior one of two ventrally placed bones in the pelvic girdle of vertebrate animals above the fishes.

Pulmonary circulation. The circulation of the blood through the lungs, as distinguished from that through the body in general (systemic).

Pulsating vacuole. Same as **contractile vacuole.**

Pupa. A quiescent stage in the development of an insect, just before the adult condition is reached.

Purkinje, Jan Evangelista (*poor keen′ ya*). Bohemian physiologist in the University of Prague, 1787–1869.

Pylorus (*pi lo′ rus*). The opening from the stomach to the intestine.

Pyrenoid (*pi re′ noid*). A small protein body found enclosed in some cells.

Quadrate. One of the bones of the skull; in birds and reptiles and bony fishes, the bone from which the lower jaw is suspended.

Quaternary (*kwa ter′ na ri*). A division of Cenozoic time later than the Tertiary.

Race. A group of individuals having certain characteristics in common because of common ancestry.

Radial canal. One of four tubes extending from the middle to the margin of a medusa.

Radial symmetry. An arrangement of the parts of an object or organism such that it is capable of being divided into halves that are mirrored images of one another, by two or more planes all of which pass through a common longitudinal axis.

Radiating canal. One of a series of collecting channels surrounding the pulsating vacuoles of Paramecium and similar protozoa.

Radio-ulna. The fused radius and ulna of frogs and toads.

Radius. The bone of the lower arm located on the thumb side in Amphibia and the higher vertebrates.

Rana. A genus of frogs. **R. cantabrigenesis,** the wood frog; **R. catesbeiana,** bull frog; **R. clamitans,** green frog; **R. palustris,** pickerel frog; **R. pipiens,** leopard frog.

Range. The area occupied by a species or larger taxonomic group of animals or plants.

Ray, John. English naturalist, 1627–1705.

Reaction. Any response of an animal to a stimulus.

Recapitulation theory. See **biogenetic law.**

Receptacula seminis (*res' ep tak' u la sem' i nis*). Chambers in which one animal stores sperms received from another.

Recessive. Not being produced when the gene for a contrasted dominant character is also present; said of inherited characters that are concealed in heterozygotes.

Reciprocal. Involving the same types of individuals, but with the sexes reversed; said of two crosses, in one of which the female possesses the same characteristic as does the male in the other cross.

Rectum. The terminal portion of the large intestine in the higher vertebrates. In vertebrates with a cloaca, the term is sometimes applied to the part of the large intestine anterior to the cloaca.

Redi, Francesco (*ra' dee*). An Italian naturalist and poet, 1626–1697.

Reductase (*re duk' tase*). An enzyme which brings about reduction, or the removal of oxygen or combination of hydrogen.

Reduction. Cell division in which chromosomes are not split, but merely separated from one another after having previously come together in pairs, as occurs in one of the two maturation divisions in bisexual reproduction.

Reflex. Same as **reflex action.**

Reflex action. An action performed as a result of an impulse which passes over a reflex arc. It is involuntary and is often performed without the consciousness of the organism.

Reflex arc. A group of two or more neurons, one of them sensory, another motor, so connected as to be able to transmit impulses resulting in reflex actions.

Regeneration. The production of lost parts by organisms.

Remak, Robert (*re mahk'*). A German neurologist, 1815–1865.

Rennin. An enzyme produced by the gastric glands and having the property of coagulating milk.

Reproduction. The formation of new individuals among organisms.

Reptilia. A class of vertebrate animals including the snakes, lizards, crocodiles, turtles,and some others. For definition see Chap. XIII.

Respiration. The gaseous metabolism of protoplasm, including elimination of carbon dioxide, usually absorption of oxygen, and, according to some physiologists, the chemical reactions which consume oxygen or produce carbon dioxide.

Retina (*ret' i na*). The sensitive inner layer of the eye of vertebrates and some other animals.

Retractile. Capable of being withdrawn.

Rhabdocœle (*rab' do seel*). A flatworm (Platyhelminthes) of the order Rhabdocœlida.

Rhinozoa (*ri' no zo' a*). A group of animals (literally nose animals) in Oken's early classification. It comprised the reptiles.

Rhizopoda (*ri zop' o da*). A class of Protozoa having a form that is changeable through the production of pseudopodia; example, Amœba.

Rhynchocephalia (*ring' ko se fa' li a*). An order of Reptilia, comprising only one living form, Sphenodon, of the New Zealand region.

Rodent. A gnawing mammal, a member of the order Rodentia (rats, mice, rabbits, squirrels, etc.).

Rodentia. The order of mammals including the rodents (rats, mice, squirrels, etc.).

Rotifera (*ro tif' er a*). A group of animals (the rotifers) usually regarded as a separate phylum, but of uncertain position in the animal kingdom. For definition see Chap. XIII.

Sacculina (*sak' ku li' na*). A degenerate crustacean, related to the barnacles, parasitic on crabs.

Sacral. Pertaining to the sacrum, the region between the hips.

Sacrum. A group of vertebræ, more or less fused, in the region between the hips.

Sagitta (*sa jit' ta*). A marine animal of small size, sometimes called the arrow worm, but not a true worm at all. Its relationship to other animals is obscure.

Salientia (*sa' li en' shi a*). An order of Amphibia including the tailless forms (frogs, toads).

Saliva. The fluid secreted by the salivary glands about the mouth.

Salivary. Pertaining to saliva, the fluid secreted into the mouth in mammals.

Salvelinus fontinalis (*sal' ve li' nus fon' ti na' lis*). A species of trout.

Sarcode. The term first applied to protoplasm by Felix Dujardin.

Sarcolemma. The membrane surrounding a striated muscle cell.

Sarcoplasm. The protoplasm of a striated muscle cell, as distinguished from the enclosed sarcostyles.

Sarcostyle. One of the longitudinal fibrils or contractile elements of a striated muscle cell. In it the light and dark bands characteristic of such muscle are located.

Scaphiopus (*ska fi' o pus*). A genus of spadefoot toads.

Scaphites (*skaf i' teez*). A genus of extinct cephalopods of the ammonitic form.

Scaphopoda (*skaf op' o da*). A class of Mollusca in which the shell and mantle are tubular, as in Dentalium.

Scapula. The shoulder blade; a bone of the pectoral girdle, located on or near the dorsal side of the body.

Schleiden, Matthias (*shli' den*). German botanist, 1804–1881.

Schneider, C. (*shni' der*). A German biologist.

Schultze, Max (*shoolt' sa*). German biologist and anatomist, 1825–1874.

Schwann, Theodor (*shvahn*). German physiologist and anatomist, 1810–1882.

Sciuridæ (*si u' ri dee*). The family of rodents including the flying squirrels, squirrels, marmots, and chipmunks.

Sciurinæ (*si' u ri' nee*). The subfamily of Sciuridæ comprising the marmots, squirrels, and chipmunks.

Sciuromorpha (*si' u ro mor' fa*). The suborder of rodents comprising the squirrel-like forms.

Sciurus (*si u' rus*). The genus including the arboreal squirrels.

Scolex. The enlarged attaching organ from which are budded off the proglottides of a tapeworm chain.

Scyphozoa (*si' fo zo' a*). A class of Cœlenterata, jellyfishes of large size which have no hydroid form in the life cycle.

Secondary. For application to spermatocytes, see **spermatocyte.** For application to oöcytes, see **oöcyte.**

Secretin (*se kre' tin*). A substance produced in the small intestine and serving to stimulate secretion by the pancreas and liver.

Secretion. The act of producing from the blood or other fluids or substances in the protoplasm some new material to be used in metabolism or otherwise. Also the new substance thus formed.

Sedimentary. Formed from sediment; said of rocks originally deposited under water, and now found in layers.

Segmentation. Same as **cleavage.**

Segregation. The separation of the genes of a homologous pair at the time of maturation of the germ cells, or at some other time, so that each germ cell receives only one member of the pair. Sometimes applied also to the independent distribution of genes of different pairs to the germ cells.

Self-fertilize. To fertilize the eggs of an individual by spermatozoa of the same individual.

Semicircular canal. One of several curved tubes forming part of the inner division of the ear in vertebrates.

Seminal receptacle. A organ in a female animal for the reception and storage of spermatozoa from the male.

Seminal vesicle. One of several bodies closely connected with the testes in the earthworm, in which a large part of the development of the spermatozoa takes place. Also, an enlargement in the vas deferens or similar duct in which spermatozoa may be stored in various animals.

Semipermeable. Permitting the passage of solvents but preventing the passage of dissolved substances.

Sensory. Pertaining to sensation; applied to a neuron which transmits an impulse resulting in sensation, or by extension to any other receiving neuron whether concerned with sensation or not.

Septum. A partition.

Sessile. Attached directly, as distinguished from stalked. Sometimes, also, attached, as distinguished from free-living.

Seta (*pl.*, **setæ**, *se' tee*). A spine; specifically, one of the spines projecting from the somites of an earthworm and used for locomotion.

Severino, Marco Aurelio (*sev' er ee' no*). Italian physician, professor in University of Naples, 1580–1656.

Sex-linked. Associated with sex; said of hereditary characters the factors for which are in the x-chromosomes associated with sex.

Sexual. Involving the production of true germ cells, or the fusion of nuclei; said of reproduction, or of an individual employing such a mode of reproduction.

Sexual selection. The supposed preference of animals of one sex for certain qualities in the other sex, leading to the preservation of those qualities in later generations.

Shoal. A shallow place in a body of water; also a sandbank or bar which makes the water shallow.

Siagonodon (*si' a gon' o don*). A genus of snakes.

Silurian. Of middle Paleozoic time, between Ordovician and Devonian.

Siphon. A passageway for currents of water; as the clefts between the halves of the mantle of mussels where the edges do not meet, or the tube on the ventral side of a squid or cuttlefish.

Siphonophora (*si' fo nof' o ra*). An order of Hydrozoa (Cœlenterata), the members of which form highly polymorphic colonies (e.g., Physalia, the Portuguese man-of-war).

Siphonops (*si' fo nops*). A genus of cœcilians (Apoda, Amphibia).

Siren. A genus of salamanders.

Slime tube. A sheath of mucous material secreted on the surface of an earthworm at the time of mating.

Small intestine. That part of the intestine of vertebrates immediately following the stomach, as distinguished from the large intestine.

Smooth muscle. Muscle composed of non-striated, uninucleate, spindle-shaped cells. It is common in the intestine, bladder and glands of vertebrates.

Solanum (*so la' num*). A genus of plants including the common potato, nightshade, and many others.

Solute (*so lute'*). A dissolved substance.

Solution (*so lu' shun*). A liquid containing another substance in the form of particles not greater than molecules in size.

Solvent. A liquid in which another substance is, or may be, dissolved.

Soma. The body, as contrasted with the germ cells.

Somatic. Pertaining to the body; when applied to cells, referring to the sterile body cells in contrast to the germ cells which are reproductive.

Somite. One of the segments into which the body of a worm or arthropod or other segmented animal is divided.

Spallanzani, Lazaro (*spahl' lahn dzah' ne*). Italian naturalist and physiologist, 1729–1799.

Species (*pl.*, **species**). A group of animals or plants so nearly alike that, in general, they might have sprung from the same parents. (The term is rather arbitrarily used, however.)

Specific. Pertaining to a species.

Sperm. One of the male germ cells in an animal or plant; also called sperm cell.

Spermaducal pore. One of the two prominent openings through which spermatozoa issue from the earthworm and similar animals. In the common earthworm they are situated on the fifteenth metamere.

Spermary. See **testis.**

Spermatheca. See **seminal receptacle.**

Spermatid. One of the two cells formed by the second maturation division of the male germ cells. By transformation in shape the spermatids become mature spermatozoa.

Spermatocyte (*sper' ma to site*). A male germ cell between the beginning of maturation and the second maturation division. A spermatocyte is called **primary** during the growth period and prior to the first maturation division; **secondary** after the first division but prior to the second.

Spermatogenesis (*sper' ma to jen' e sis*). The maturation of male germ cells.

Spermatogonium (*sper' ma to go' ni um*) (*pl.*, **spermatogonia**). One of the early germ cells of a male animal, prior to the beginning of maturation.

Spermatophore (*sper' ma to fore*). A mass of spermatozoa, sometimes resting upon a stalk or being otherwise attached, as in some salamanders.

Spermatozoön (*sper' ma to zo' on*) (*pl.*, **spermatozoa**). The male germ cell in animals.

Sphenodon (*sfen' o don*). A genus of reptiles of the order Rhynchocephalia. But one living species is known.

Spheroid. Of nearly spherical shape.

Spicule. A body of various shapes commonly of calcareous or siliceous material, forming part of the skeleton of a sponge.

Spinal cord. That part of the central nervous system of vertebrate animals lying behind the brain and largely enclosed in a channel in the vertebræ.

Spindle. A group of structures resembling threads, in the form of a spindle, formed in the cytoplasm of a cell during mitosis.

Spiracle. In frog tadpoles, an opening through which water passes out of the gill chamber on one side. In insects, one of a number of openings on the sides of the body through which air is introduced to the tracheæ.

Spireme (*spi' reem*). The coiled or tangled thread formed by the chromatin of a cell prior to division.

Spirostomum (*spi ros' to mum*). A genus of ciliated protozoa.

Splint. A bone at either side of the foot of the horse and some of its relatives, being the remnant of a lost toe.

Spongilla. A genus of freshwater sponges.

Spongin. The horny material of the skeleton of the bath sponges.

Spontaneous generation. Same as **abiogenesis.**

Sporadic. Occurring at irregular intervals, often without apparent reason; said of migration of animals.

Spore. One of a great variety of reproductive cells usually having protective coverings. Often the term is limited to asexual reproductive cells. The word is often compounded with qualifying prefixes, or preceded by qualifying adjectives.

Sporozoa. A class of protozoa, parasites usually without locomotor organs or mouth.

Sporulation. The formation of spores; sometimes applied to multiple division of the nucleus followed by fragmentation of the cytoplasm, which occurs in the spore formation of certain species.

Squamosal. A bone of the postero-lateral region of the skull of vertebrates. In the mammals it suspends the lower jaw, but not in the other vertebrates.

Squamous epithelium (*skwa′ mus*). Epithelium whose cells are low and flat.

Statoblast (*stat′ o blast*). A gemmule-like body by means of which many Bryozoa reproduce asexually.

Steapsin (*ste ap′ sin*). The fat-splitting enzyme of the pancreatic fluid.

Stearic (*ste ar′ ik*). One of the very common fatty acids.

Stegocephali (*steg′ o sef′ a li*). A group of extinct armored Amphibia of large size.

Stegodon (*steg′ o don*). A genus of extinct animals, ancestral to the elephants, from the Pliocene of southern Asia.

Stegosaurus (*steg′ o saw′ rus*). A genus of dinosaurs bearing rows of plates set vertically on the back; belonging to Jurassic and Comanchian time.

Stejneger (*sti′ ne ger*). A living American herpetologist.

Stentor. A genus of ciliated protozoa.

Sternum. The breastbone; present in most vertebrates except fishes and some reptiles.

Stigma. A pigment spot in certain unicellular organisms, sometimes regarded as light-perceptive. Also, the part of the pistil of a flower which receives the pollen.

Stimulus. A change in the environment or some internal condition which produces a reaction in an organism.

Stomach. An enlargement in the anterior part of the digestive tract of many animals; certain phases of the digestion of food occur there.

Storeria. A genus of snakes. **S. occipitomaculata** (*ok sip′ i to mak′ u la′ ta*); **S. dekayi** (*de kay′ i*).

Stratified. Arranged in strata or layers; said of epithelia, geological deposits, etc.

Stratum (*pl.*, **strata**). A layer; specifically, a layer of sedimentary rock.

Stratum corneum. The thin outermost layer of cells in the skin of certain animals (as the frog).

Striated muscle. Muscle composed of cylindrical, cross-banded, multinucleate cells (except in the heart). Skeletal muscles in vertebrates are of this kind.

Striation. A stripe; as the cross-lines of voluntary muscle cells.

Structural formula. A formula designed to show the arrangement of atoms in the molecule of a chemical substance. Also called graphic formula.

Stylonychia (*sti′ lo nik′ i a*). A genus of ciliated protozoa.

Subepithelial cells. In Hydra, rounded cells lodged among the epithelial cells, often near the base of the latter.

Succus entericus. The fluid secreted by the small intestine.

Sucker. An attaching organ beneath the head of a frog tadpole; a similar organ on the scolex of a tapeworm colony; also the attaching organ of leeches.

Suctoria. A class of ciliated protozoa which bear no cilia when adult, but have tube-like tentacles.

Suspension. A mixture of fine solid particles in a liquid.

Suspensoid. A mixture consisting of a liquid in which are distributed solid particles that are exceedingly minute yet larger than molecules.

Sustentative (*sus ten′ ta tiv*). Supporting; applied to connective tissue and other supporting tissues.

Suture. The line of junction between a septum of a cephalopod shell and the outer wall of the shell. Also the immovable joint between two flattened bones, as those of the skull.

Swammerdam, Jan (*swahm′ mer dahm*). Dutch naturalist, anatomist and entomologist, 1637–1680.

Symbiosis (*sim′ bi o′ sis*). The association of two species of animals for their mutual benefit.

Symbiote. An animal which lives in a symbiotic relationship with another species; called also symbiont.

Symbiotic. Of the nature of symbiosis.

Symmetrical. Of a form that may be divided by a line or plane into two parts which are mirrored images of each other.

Symmetry. The state of being symmetrical.

Sympathetic nervous system. Two longitudinal nerve cords and associated ganglia in the dorsal region of vertebrates.

Sympheidole (*sim' fi do' le*). A genus of ants.

Synapse (*sin' aps*). The point of contact of two neurons.

Synapsis (*sin ap' sis*). The pairing of maternal with paternal chromosomes early in the maturation of the germ cells.

Synapta. A genus of sea cucumbers.

Syncytium (*sin sish' i um*). An undivided mass of protoplasm containing several or many nuclei.

Syncœcy (*sin ee' si*). The dwelling together of two species, of which one is benefited by the relationship, the other neither harmed nor benefited.

Synura. A genus of colonial flagellate protozoa.

System. A collection of organs concerned with the same general function, as digestion.

Systematic zoölogy. See **taxonomy.**

Systemic circulation. The circulation of the blood through the body in general, as distinguished from that through the lungs or lungs and skin (pulmonary or pulmocutaneous).

Tadpole. The larva of a frog, toad, or certain other animals.

Tail. A slender posterior appendage. In a spermatozoön, the whip-like propelling organ behind the head and mid-piece.

Tamiasciurus (*ta' mi a si u' rus*). The subgenus of the genus Sciurus including the red squirrels. **Sciurus (Tamiasciurus) hudsonicus loquax** (*hud son' i kus lo'-kwaks*), the southern Hudsonian red squirrel.

Tarsal. One of a number of bones in the ankle of most vertebrate animals.

Tarsometatarsus (*tar' so met' a tar' sus*). A compound bone in the leg of a bird, formed of several of the metatarsals and tarsals.

Taxis. An orientation of an organism with reference to a stimulus.

Taxonomy. The science of the classification of animals or plants.

Teleostomi (*te' le os' to mi*). A subclass of Pisces comprising the true fishes. They have a skeleton partly or wholly of bone, and respire by means of gills.

Telolecithal (*tel' o les' i thal*). Having the yolk massed toward one side; said of eggs in which the yolk is most abundant in the vegetative half.

Telophase (*tel' o faze*). The final phase of mitotic cell division, in which the nuclei are reconstructed.

Tentacle. One of a number of arm-like projections from hydroids, Bryozoa, Nautilus, and other animals. Also one of certain elongated individuals of a siphonophore colony.

Tentaculate. Bearing tentacles.

Terrapene (*ter' a pee' nee*). A genus of turtles of the family Testudinidæ.

Terrigenous (*ter rij' e nus*). Derived from the land; as applied to lake bottoms, composed of material washed in from the land, as distinguished from material of organic origin.

Tertiary (*ter' shi a ri*). The earlier of two divisions of Cenozoic time.

Test. A hard outer covering, capsule, or shell; as of a sea urchin.

Testis. The organ in which male germ cells are lodged and developed.

Testudinata (*tes tu′ di na′ ta*). An order of reptiles, comprising the turtles.

Testudinidæ (*tes′ tu din′ i dee*). A family of turtles.

Tetrad. A quadruple body formed, during the growth period in the maturation of germ cells, from the union of two chromosomes which at the same time divide in two.

Thales (*tha′ leez*). A Greek philosopher and astronomer who lived about 640–546 B.C.

Thamnophis (*tham′ no fis*). A genus of garter snakes. **T. butleri** (*but′ ler i*); **T. proximus** (*proks′ i mus*); **T. sackeni** (*sak′ en i*); **T. sauritus** (*saw ri′ tus*).

Thermotaxis (*ther′ mo taks′ is*). A response to temperature.

Thermotropism (*ther mot′ ro piz′m*). The response of an organism to temperature.

Thigmotaxis (*thig′ mo taks′ is*). An orientation of an organism with reference to a contact stimulus.

Thigmotropism (*thig mot′ ro piz′m*). The response of an organism to the stimulus of contact.

Thoracic. Pertaining to the thorax or chest.

Thorax. A middle portion of the body of many animals, between head and abdomen.

Thricozoa (*thrik′ o zo′ a*). A class of animals (hair animals) in Oken's early classification. It comprised the mammals which Oken also called Ophthalmozoa.

Thymus. A ductless gland located near the gill clefts, or in the neck, or in the anterior part of the thorax in various vertebrates.

Thyroid. A ductless gland located in the ventral part of the pharynx.

Tibia. The inner one of the two bones in the lower leg of vertebrates, except the fishes.

Tibiofibula. The fused tibia and fibula of some Amphibia.

Tibiotarsus. A compound bone in the leg of a bird, formed of the tibia and certain of the tarsal bones.

Tissue. A group of cells of similar structure forming a continuous mass or layer.

Tonsil. A glandular organ at the side of the throat.

Tonus. A state of continuous activity, as in muscle.

Trachea (*tra′ ke a*). The tube conveying air to and from the lungs in vertebrates. Also an air tube in insects and some other invertebrates.

Tracheal gills. Thread-like or leaf-like projections in which tracheæ have their beginning in certain aquatic insect larvæ.

Trachelocerca (*tra′ ke lo ser′ ka*). A genus of ciliated protozoa.

Transverse process. One of a pair of projections at the sides of a vertebra in most vertebrate animals.

Trematoda (*trem′ a to′ da*). A class of Platyhelminthes, parasitic flatworms with suckers and without cilia.

Triassic. Of the earliest Mesozoic time.

Triceratops (*tri ser′ a tops*). A genus of three-horned dinosaurs of late Cretaceous time in western North America.

Trichinella (*trik′ i nel′ la*). A genus of parasitic roundworms, the cause of the disease trichinosis.

Triclad. Having the digestive tract divided into three branches; said of an order of flatworms.

Trilophodon (*tri lo′ fo don*). An extinct genus of animals from the Miocene of several continents; probably an ancestor of the elephants.

Trionychidæ (*tri′ o nik′ i dee*). A family of turtles.

Tripalmitin. A fat composed of glycerol and three molecules of palmitic acid; the most abundant fat in man.

Triploblastic (*trip′ lo blas′ tik*). Composed of three fundamental layers of cells.

Triturus. A genus of salamanders.

Tropism (*tro′ piz′m*). A response of an organism to a stimulus.

Trypsin. A proteolytic enzyme produced by the pancreas.

Trypsinogen (*trip sin' o jen*). The inactive substance from which the enzyme trypsin is produced.

Tryptic. Of the nature of trypsin; said of proteolytic enzymes that act in an alkaline medium.

Tube feet. Tubular protrusions from the arms of echinoderms, which serve as organs of locomotion.

Tubercula pubertatis (*tu ber' ku la pu' ber ta' tis*). Two thick glandular ridges on the clitellum of an earthworm near the ventral surface.

Tuberculate. Bearing cusps or conical prominences; said of teeth.

Tubifex. A genus of freshwater annelid worms.

Tubular gland. A gland whose lumen is of about uniform bore throughout.

Tundra. A level or undulating treeless plain of the arctic region.

Tunicata (*tu' ni ka' ta*). A subphylum of Chordata, including the sea squirts, sea pork, salpas, etc. For definition see Chap. XIII.

Turbellaria (*tur' bel la' ri a*). A class of Platyhelminthes, ciliated flatworms leading a free existence.

Tympanum (*tim' pa num*). The middle ear; also the membrane separating the middle from the outer ear.

Tyndall, John (*tin' dal*). British physicist, 1820–1893.

Type. In systematic zoölogy, an individual or group which is formally held to be typical of the species or larger group to which it belongs; as, the type specimen of a species, the type species of a genus, or the type genus of a family.

Typhlosole (*tif' lo sole*). A ridge resulting from the infolding of the dorsal intestinal wall of the earthworm.

Ulna. The bone of the little finger side of the fore arm in Amphibia and the higher vertebrates.

Umbilical cord. A rope-like cord in which blood vessels pass between an embryo and the placenta in viviparous animals.

Ungulata. A group of mammals to which the hoofed animals (pigs, sheep, horses, elephants, etc.) belong.

Ungulate. One of the Ungulata.

Uniformitarianism. The doctrine that geological processes of the past were similar to those of the present time.

Unio. A genus of freshwater mussels.

Unisexual. Involving but one sex, the female; applied to parthenogenetic reproduction.

Unit character. A hereditary trait that behaves as a unit in transmission, being capable of inheritance independently of other unit characters.

Universal symmetry. An arrangement of the parts of an object or organism such that it is capable of being divided into symmetrical halves by an indefinite number of planes passing in any direction through a central point.

Urea (*u re' a*). A substance, $CO(NH_2)_2$, produced by the decomposition of proteins and some other substances in organisms.

Ureter (*u re' ter*). A tube conducting urine away from the kidney.

Urethra (*u re' thra*). The duct by which urine is discharged from the bladder.

Urinary bladder. A bag in which urine is stored.

Uriniferous tubule. One of many coiled tubes making up the bulk of the kidney in vertebrates.

Urinogenital system. A group of organs concerned with both excretion and reproduction in vertebrates.

Uroglena (*u' ro gle' na*). A genus of flagellate Protozoa in which free-swimming spherical colonies are embedded in a gelatinous substance.

Uterus (*u' te rus*). A modified portion of the oviduct in which the eggs undergo at least part of their development. Strictly the term uterus is applicable only in animals in which the developing embryo becomes attached to the wall of the organ.

Vacuole. A region within a cell occupied by a liquid other than protoplasm, usually water with various substances in solution.

Vagina. The passage leading from the uterus to the exterior in many animals.

Variation. In biology, the occurrence of differences among the individuals of the same species; also, sometimes, among the individuals or species of larger groups (genera, families, etc.).

Variety. In taxonomy, a division of a species; a group of individuals within a species that differ in some minor respect from the rest of the species.

Vas deferens (*vas' def' er enz*) (*pl.*, **vasa deferentia,** *vas' a def' er en' shi a*). A duct conveying spermatozoa from the testis to the exterior.

Vas efferens (*vas' ef' fer enz*) (*pl.*, **vasa efferentia,** *vas' a ef' fer en' shi a*). One of a number of minute tubes leading away from a testis, serving to convey the spermatozoa. They lead into a larger tube called in many cases the vas deferens.

Vascular tissue. Blood or lymph.

Vegetative. Concerned with nutrition. When applied to an egg, meaning that side near which the yolk is accumulated (vegetative pole).

Vein. A vessel conveying toward the heart blood which has already traversed capillaries since leaving the heart.

Velum. A horizontal circular shelf within the margin of a medusa.

Ventrad. In a ventral direction.

Ventral. Literally, pertaining to the belly; hence, usually, lower.

Ventricle. The posterior chamber of the heart in fishes, Amphibia and some reptiles, and one of the two posterior chambers in higher vertebrates. Its function is the propulsion of the blood through the main arteries and connecting vessels.

Vermiform appendix. A narrow blind pouch forming a prolongation of the cæcum.

Vertebrata. A subphylum of the phylum Chordata, comprising the backboned animals. For definition see Chap. XIII.

Vertebrate. *adj.* Possessing a backbone. *n.* An animal having a backbone.

Vesalius (*ve sa' li us*). A Belgian anatomist and court physician who lived 1514–1564.

Vicq d'Azyr, Felix (*veek' da zeer'*). French comparative anatomist and physiologist, 1748–1794.

Vicuna (*ve koon' ya*). A llama-like animal of South America.

Virchow, Rudolf (*veer'* HO). A German physiologist and pathologist, 1821–1902.

Visceral. Pertaining to the viscera, or organs contained in some large cavity of the body; applied in the vertebrates chiefly to the organs of the abdomen, in clams to the digestive organs and glands above the foot.

Viscosity. The resistance offered by a substance to the relative movement of its molecules.

Visual. Pertaining to the sense of sight.

Vitamine. One of several substances common in leafy vegetables, animal fats, and elsewhere, which are necessary for proper metabolism in animals. Their chemical nature is mostly unknown.

Viviparity (*viv' i par' i ti*). The condition of being viviparous.

Viviparous (*vi vip' a rus*). Producing young from eggs that are retained in the uterus of the mother, with the aid of nutrition derived from the mother through a placenta and umbilical cord.

Vocal cords. Membranous folds stretched across the larynx, which by their vibrations in forced currents of air cause the voice.

Volvocales (*vol′ vo ka′ leez*). An order of plants including Volvox, Pandorina, Eudorina, etc.

Volvox. A small spherical organism composed of flagellated green cells embedded in jelly, in a single layer around a liquid interior. Sometimes regarded as an animal, though more properly included among plants. **V. aureus** (*aw′ re us*) of small size; **V. rousseletii** (*roo′ se let′ i i*) very large; **V. perglobator** (*per′ glo ba′-ter*).

Vorticella. A ciliated protozoön attached to a contractile stalk.

Vorticellidæ (*vor′ ti sel′ li dee*). A family of ciliated protozoa to which Vorticella, Epistylis, Carchesium and Zoöthamnium belong.

Wallace, Alfred Russel. English naturalist, 1823–1913.

Xanthophyll (*zan′ tho fil*). One of two yellow substances associated with chlorophyll.

X-chromosome. A chromosome closely associated with the determination of sex. In many animals the female has two of them, the male only one.

Xenophanes (*ze nof′ a neez*). A Greek philosopher who lived about 570–480 B.C.

Xerophthalmia (*ze′ rof thal′ mi a*). A dry lusterless condition of the eyeball.

Y-chromosome. A chromosome possessed only by the males of many species. It behaves in maturation much as if it were homologous with the x-chromosome.

Yolk plug. The remnant of the vegetative cells last to be drawn into the interior of a gastrula in certain telolecithal embryos.

Yucca. A genus of liliaceous plants having long pointed stiff leaves and a panicle of white flowers.

Zoögeography. The branch of zoölogy treating of the geographical distribution of animals.

Zooid. One of the members of a hydroid or siphonophore colony. Often, in a restricted sense, a particular kind of individual, as a hydranth.

Zoölogy. The science of animals.

Zoöthamnium (*zo′ o tham′ ni um*). A genus of colonial ciliated protozoa, resembling Vorticella.

Zygapophysis (*zi′ ga pof′ i sis*). One of four short projections, two in front and two behind, extending from the upper portion of a vertebra. Those of the posterior pair articulate with the anterior pair of the vertebra next behind.

Zygote. A cell or individual produced by the fusion of two cells or their nuclei in the process of sexual reproduction.

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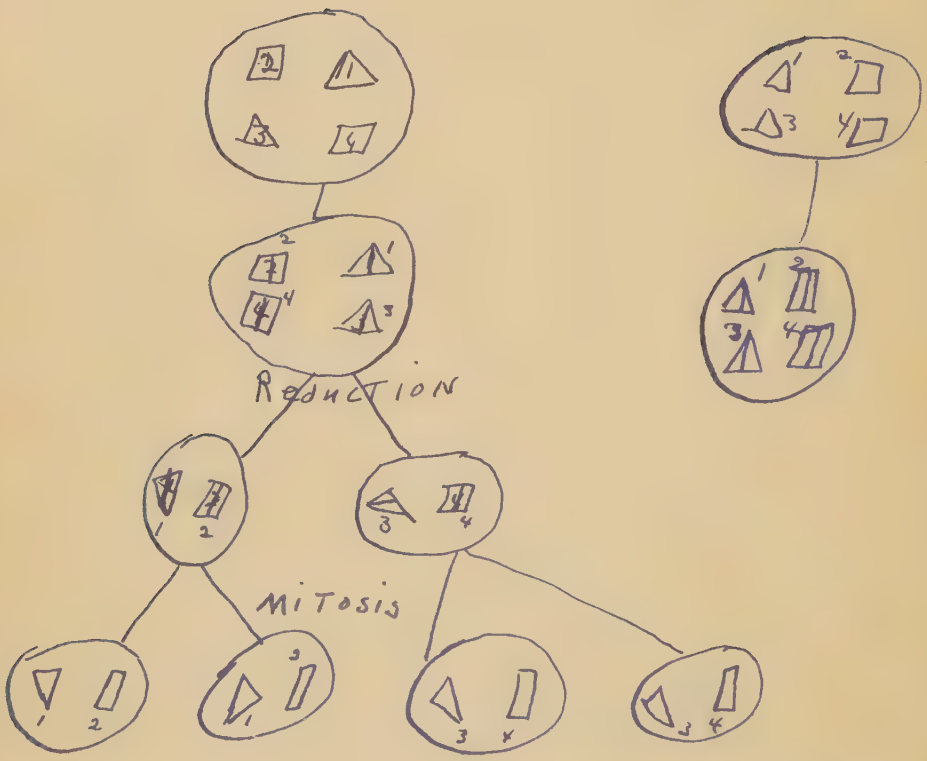
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